

Towards solving Darwin's "mystery": Speciation and radiation in lacustrine and riverine freshwater gastropods*

Matthias Glaubrecht

Museum für Naturkunde, Leibniz Institute for Research in Evolution and Biodiversity at the Humboldt University Berlin, Invalidenstrasse 43, D-10115 Berlin, Germany

Correspondence, M. Glaubrecht: matthias.glaubrecht@mfn-berlin.de

Abstract: As much as the century-long debate on what species are has created confusion and controversy, not less has speciation been discussed, *i.e.*, the process of how new forms and taxa evolve, ultimately resulting in the multiplication of species. Darwin's often cited "*mystery of the mysteries*", *i.e.*, the origin of species and, as a consequence, of biological diversity in general, remains at the forefront of current evolutionary biology. While allopatric speciation by geographical separation is still considered an important mechanism in most cases, recently it became evident (as a slow and quiet revolution) that alternative explanations may account for how new species come into being. Among the most prominent factors, particularly in the context of adaptive radiation, is ecology in concert with specialization, albeit not necessarily in a sympatric setting. Unfortunately, for freshwater gastropods we are far away from really understanding the details of the various speciation processes (allopatric versus sympatric) and the role of natural selection, adaptation and ecology that have lead to the array of radiations described recently for several taxa and cases. Contrasting lacustrine and riverine settings, I will discuss these issues for limnic Cerithioidean gastropods, in particular for (1) paludomids from East Africa (*i.e.*, the thalassoid species from Lake Tanganyika and *Potadomoides* Leloup, 1953 in the Congo River system), (2) pachychilids *Tylomelania* Sarasin and Sarasin, 1897 endemic to lakes on Sulawesi in Indonesia, (3) *Brotia* H. Adams, 1866 in the Kaek River drainage in Thailand, and (4) *Madagasikara* Köhler and Glaubrecht, 2010 on Madagascar. With an increasing armamentarium of molecular genetic techniques for exploring the genetic structure of populations and species, the one mystery has become many, and possible solutions multiplied, as we uncover further complexities in what species really are and how they multiply.

Key words: phylogenetic pattern, fossils, microevolutionary studies, Lake Tanganyika, Congo River, Lake Turkana

"These facts seemed to me to throw some light on the origin of species – that mystery of mysteries, as it has been called by one of our greatest philosophers." Darwin (1859: 1)

Albeit often ignored, Jean Baptiste de Lamarck's (1809) proposal that species change through time and that fossils represent ancestors of living species can be seen as the first consistent theory of genuine evolutionary change (Mayr 1982, Corsi 1988). Although Lamarck's ideas on the origin of species were widely known and discussed, they were largely dismissed. As many biographers have pointed out (*e.g.*, Desmond and Moore 1991, Browne 2002), even Charles Darwin later in his life denied any influence of Lamarck on his own thinking about variational evolution and the very process that brings species about. In his epochal "*Origin of Species*", Darwin (1859) depicted one diagrammatic sketch of a hypothetical phylogenetic tree to illustrate and explain, as we understand today, biological diversity as the result of descent with modification and a continuous process leading to a branching pattern, namely speciation as we call it today.

Since then evolutionary trees have become the lingua franca of biology. Throughout the history of systematics and evolutionary biology there has been no shortage of attempts to find a classification system that captures the diversity of living forms in nature (*see, e.g.*, historical review and references in Endersby 2009, Glaubrecht and Haffer 2010). What Charles Darwin (1859) once called the "*mystery of the mysteries*", *i.e.*, the origin of species and, as a consequence, of biological diversity in general, remains at the forefront of current evolutionary biology. Therefore, the fundamental question as to how new species evolve is one of the six "*Darwinian mysteries*", or big questions in evolutionary biology and biodiversity, all still in need of answering (Glaubrecht 2009).

In this context, it is important to realize the two focal points of evolutionary biology, anagenesis, *viz.* natural selection acting to transform existing taxa, versus cladogenesis, or the actual multiplication of species. Introducing the concept of natural selection, Darwin's work is justifiable marvelled as brilliant induction in presenting insightful

* From the "Symposium on Speciation in Molluscs" presented at the meeting of the American Malacological Society on 20 July 2009 in Ithaca, New York. All manuscripts were reviewed and accepted by the Guest Editor, Dr. Warren Allmon.

examples of adaptation and anagenesis. “*I am convinced that Natural Selection has been the main but not exclusive means of modification*”, he wrote in the introduction to his book on the “*Origin of Species*” (Darwin 1859: 6). However, Darwin struggled in vain with the question of the multiplication of species or cladogenesis. It was Mayr’s (1942, 1963) syntheses, including the formulation of the concepts both of biological species and allopatric speciation, that finally and for long provided an explanation for cladogenesis, grounded chiefly in geography, as a factor largely ignored before.

ON SPECIES AND SPECIATION

Speciation, arguably the fundamental step in cladogenesis, is a key process in evolutionary biology with paramount consequences for systematics, genetics and ecology. Its study, including historical and ecological aspects, is one of the most active research field in evolutionary biology, with the development of testable criteria for distinguishing alternative hypotheses (for the most recent reviews see, e.g., Coyne and Orr 2004, Gavrilets 2004, Mallet 2008a, Nosil 2008, Butlin *et al.* 2009, Schluter 2009).

Most essential in this context is, of course, our perception of species as being of major importance for biology in general and evolutionary studies in particular. The debate on speciation is firmly entangled with the so-called “species-problem”. As, for example, the biological species concept is explicitly related to the process of speciation, this and other concepts determine how speciation is studied. Coyne and Orr (2004) have shown how to distinguish alternative hypotheses about this process. The question of delimiting vs. defining species is currently seeing a remarkable renaissance; yet, no consensus on the nature of species has been reached, and intensive debates about species concepts continue. For a discussion of the frequent confusion of species concepts, species categories and the species taxon see, e.g., Bock (2004). For the most recent reviews on the species problem, see Hey *et al.* (2003), Sites and Marshall (2003, 2004), Coyne and Orr (2004), Glaubrecht (2004, 2009), Heuer (2008), Endersby (2009), Wilkins (2009), and Richards (2010). As Noor (2002) pointed out correctly, none of the recently suggested, lineage-based species concepts have facilitated research on the process of speciation like the biological species concept before. Only when we regard species as natural entities that have a real existence in nature, and are defined using the reproductive criterion, is the study of mechanisms of speciation a useful and potentially informative endeavour.

As much as the century-long debate on what species are has created confusion and controversy, not less has speciation been discussed as ultimately resulting in the multiplication of species. Consequently, speciation remains at the forefront of

evolutionary biology. Most generally, speciation is understood here as being caused by a change in environment, be it the establishment of geographical isolation (*i.e.*, allo- / para- and peripatry) or the onset of divergent selection in an ancestral population by sympatric speciation through ecological specialization. Barraclough (2004) has pointed out, in criticising some theoretical speciation models, that to date the role of environment has been merely considered in fixed or simple terms, thus underestimating its importance in speciation. In order to provide biologically relevant models, we need to study realistic model organisms, looking in detail into the dynamics of the underlying mechanisms of speciation and radiation. These studies involve possible links between geographical patterns and ecological processes of speciation, as well as the potential role of introgression and hybridization, and use evolutionary branching and populations genetics in a variety of spatially structured and specialized populations, combined with correlated morphological data and ecological observation, to estimate the environmental influence on speciation.

I propose that in particular those freshwater molluscs and their specific insular environments discussed in the second part of the present paper provide suitable models for this kind of study. Prior to that I will briefly review the different modes and models of speciation and hint at the relevant literature on this subject, providing an overview of our knowledge for limnic gastropods.

MODELS OF SPECIATION

“*One could not fully understand new theories unless one understood the history of the subject and the nature of the displaced theories.*” Mayr (1999: 402)

It has been proposed that in biology concepts play an equally important role as do natural laws in physics and chemistry (Mayr 1997). Given their heuristic significance, biological concepts, such as allopatric, intra-lacustrine or ecological speciation, as well as adaptive radiation or coevolution and competitive displacement, need case studies for evaluation and illustration of their general validity. Our current understanding of how species multiply was influenced by Mayr’s (1942, 1963, 1982, 2001) credo that geographic distribution and spatial isolation play a key role in allopatric speciation, and in the modern synthesis of evolution it became firmly established that geographical separation actually is a major factor in speciation (*e.g.*, Coyne and Orr 2004, Mallet 2008b, Cain and Ruse 2009).

Glaubrecht (2002, 2007a, 2007b) has outlined the historical avenues and intellectual roots of particularly the contributions of German systematists of the “Berlin School”, built by Erwin Stresemann, Bernhard Rensch and Ernst Mayr and their “new systematics”, regarded as crucial for having provided in the 1920s and 1930s the foundation for the

synthetic evolutionary theory. Summaries of knowledge on speciation were given first by Rensch (1939) and Mayr (1940). This perception of the role of the “Berlin School”, though, is largely contrary to that of, for example, Junker and Hoßfeld (2002) and Mallet (2004), who largely ignored Stressemann’s strong influence on the roots of Mayr’s thinking. However, as Cain (2009) has pointed out, it is necessary to rethink our understanding of the evolutionary synthesis. In case of Mayr at least, this would bring species again back as focal point of the evolutionary process and help to better understand the history of speciation theory, or what Mayr (1947: 263) termed “the gradual formulation of the theory of geographical speciation”.

Without doubt, modern molecular data from phylogenetic, phylogeographic and genomic studies have revealed a greater complexity of pattern and process than Mayr (1942) and subsequent researchers could ever have expected (e.g., Emerson 2008, Venditti and Pagel 2009, Venditti *et al.* 2010, Turner and Hahn 2010, for a recent example of our own species, see Presgrave and Yi 2009). In understanding evolution it has also helped to view speciation not as an endpoint but as a process. However, with the focus on factors involved in or engines powering this process, speciation is still a highly contentious issue (Hendry 2009), with allopatric versus sympatric speciation remaining one of the great controversies in evolutionary biology.

Allopatric speciation

Speciation in bisexual organisms depends on the disruption or strong limitation of gene flow between the populations involved. The simplest way to achieve this is indeed by geographic separation, with allopatric divergence being produced either by genetic drift or selection in different environments. Many observations lead to the model of allopatric speciation by Mayr (1942, 1963, 2001). For recent reviews of the various stages, see e.g., Allmon (1992) and Grant and Grant (2008).

For six decades, allopatric speciation has been the dominant concept, as the theoretical possibility of reproductive isolation in allopatry is undebated, and examples are plentiful (reviews, e.g., Barraclough and Vogler 2000, Grant 2001, Salomon 2001, Via 2001, Losos and Glor 2003, Coyne and Orr 2004, Nosil 2008, Butlin *et al.* 2009). Under the allopatric speciation paradigm, geography and its consequence, viz. blocking gene flow between populations, is regarded as the sole causation for population divergence and ultimately reproductive isolation, with spatial separation being the key. It allowed Coyne and Orr (2004) to conclude that studying speciation is largely synonymous with studying reproductive isolation. Allopatric speciation was long widely regarded as the parsimonious default or null hypothesis, and geographic mechanisms preventing interbreeding generally thought to be the most common way for new species to arise. For a contrary view, see Bush (1975, 1994, 1998), Wu (2001), Mallet (2001, 2008a, 2008b) and Johannesson (2009).

However, the perception promoted e.g., by Schuilthuis (2001) that the impact of geographical barriers has been trivial rather than paramount is misleading.

Recent advances in phylogeography provide strong support for the importance of geographical isolation in diversification and genetic differentiation. Several well-researched case-studies, e.g., so-called ring species and pairs of closely related species, indicate that incipient species formation is more complex than generally assumed, involving a number of genetically distinct components and various instances such as range contraction, isolation, differentiation, and secondary contact, even on small geographic scales. For examples, see Wake (1997), Peterson *et al.* (1999), Irwin *et al.* (2001, 2005), Grant and Grant (2008, 2009) as well as case studies compiled in Glaubrecht (2010a).

Theoretical aspects of the role of geography in speciation and its detection were explicitly discussed, for example, in Barraclough and Vogler (2000) and Losos and Glor (2003). The unsuspected complexity of allopatric speciation is particularly apparent in a special case, parapatric speciation. Usually involving an ecotone, a sharp ecological (as opposed to geographical) boundary in the distribution range of a species, a number of examples have recently emerged (Johannesson *et al.* 1995, Smith *et al.* 1997, Tatarenkov and Johannesson 1998, Schneider *et al.* 1999). Assortative mating, i.e., non-random mating due to preference for similar partners resulting in increased reproductive isolation, plays an important role, as it also does in sympatric speciation (Malausa *et al.* 2005), and its theoretical aspects have been tested in Gavrillets *et al.* (2000).

Sympatric speciation

While allopatric speciation *sensu* Ernst Mayr is still considered an important mechanism in many cases, over the last two decades alternative explanations as to how new species come into being gained more attention. As a slow and quite revolution, it became evident that an ecological rather than geographical explanation may account for speciation. In fact, as much as allopatric speciation is important in many cases, it certainly is not the only mechanism and might not even be of the eminent importance of which Mayr (2001) was convinced throughout most of his long life.

In this context the model of sympatric speciation, the evolution of reproductive incompatibility in a population with no extrinsic geographic barriers to gene flow, is contentiously discussed. As speciation models largely focus on the spatial component of speciation, the difference to which extent gene exchange and hybridization connect diverging lineages is crucial. Allopatric and sympatric speciation can be viewed as ends of a continuum defined by the amount of genetic exchange, ranging from the absence (allopatry) to substantial gene flow (sympatry). However, spatial separation and its outcome, disjunct distributions of closely

related species, might be only secondary consequences of adaptive genetic divergence under sympatric conditions, thus within a population, and not necessarily the result of passive fragmentation of populations. Recent reviews of sympatric speciation are given by Schilthuizen (2001), Via (2001), Coyne and Orr (2004), Bolnick and Fitzpatrick (2007). For a focus on theoretical models, see Gavrilets (2004).

While neither the initial theoretical demonstration of its possibility (Maynard Smith 1966, Kondrashov and Mina 1986), nor the few early case reports (*e.g.*, Bush 1969, 1975) originally had gained wide acceptance, only in recent years has the sympatric mode of speciation been reconsidered as a serious alternative based on an improved theoretical framework (Doebeli 1996, Dieckmann and Doebeli 1999, Kondrashov and Kondrashov 1999, Doebeli and Dieckmann 2003, Gavrilets 2004, Gourbiere 2004, Waga *et al.* 2007) in concert with a growing body of field evidence (Feder *et al.* 1988, Schliewen *et al.* 1994, McCune and Lovejoy 1998, Shaw *et al.* 2000, Wilson *et al.* 2000, Schliewen *et al.* 2001, Schliewen and Klee 2004, Barluenga *et al.* 2006, but see also Schliewen *et al.* 2006). However, re-evaluation of one of the famous textbook examples for sympatric speciation, the apple maggot fly *Rhagoletis*, has revealed that the picture is more complex and might also involve historical and even geographical aspects (Jiggins and Bridle 2004). Therefore, we can conclude here that sympatric speciation appears to occur in some cases, under divergent natural or sexual selection even in the presence of some gene flow. Among the most prominent factors currently discussed, particularly in the context of adaptive radiation, is ecology in concert with specialization.

Ecological speciation

An important factor involved in the formation of new species is the mechanism of initial divergence. Many evolutionary biologists, from Darwin to Mayr, were aware that ultimately speciation is also an ecological process (*e.g.*, Mayr 1947), even when later often stressing isolation as evolutionary factor (Mayr 1959). Sympatric and parapatric speciation depend on strong natural selection to work, and thus the role of adaptation has again been emphasized. Speciation involving natural selection has been termed ecological speciation by Schluter (1996). This includes but is not necessarily equal to non-allopatric speciation, with ecological specialization and both natural and sexual selection playing key roles. For a general review of the role of ecology in speciation see, *e.g.*, Orr and Smith (1998), Coyne and Orr (2004), and Butlin *et al.* (2009); for a review and discussion of the role of specialization and selection see McKinnon and Rundle (2002), McKinnon *et al.* (2004), and Irschick (2005).

Allopatric speciation is more flexible in respect to the role of selection, as random genetic processes were invoked early (peripheral isolate model, Mayr 1942) to explain the

buildup of reproductive incompatibility between separated populations. Genetic processes can lead directly to reproductive isolation, *i.e.*, without natural selection being involved. Examples are genetic drift or differential acquisition of mutations in separate populations. Nevertheless, natural selection has been regarded as the major factor in allopatric speciation as well. Under this hypothesis the build-up of reproductive isolation between populations is seen as a by-product of adaptation caused by different environmental selection pressures (Mayr 1942, Dobzhansky 1951, Endler 1986).

While de-emphasizing geographical settings and re-affirming the importance of natural selection and adaptation, ecological speciation has the same appeal of intuitive appraisal as allopatric speciation. Central to this idea is to connect differences in ecologically important traits to the build-up of reproductive isolation, thus underscoring the divergence of specific traits in the absence of the homogenizing effect of gene flow between individuals. Consequently, the prediction of the ecological model of speciation is ecologically dependent isolation. In its early stage, the theory of ecological speciation was not supported by evidence, and no tests were available to distinguish it from other modes of speciation, since several aspects of ecological speciation, as for instance possible reinforcement, can occur in the late phases of about every speciation model (Schluter 2001, Coyne and Orr 2004). It should be noted that reinforcement, *i.e.*, the enhancement of (pre-) zygotic isolation in sympatry, or natural selection against maladaptive hybridization (Coyne and Orr 2004) results in rapid allopatric speciation on the one hand (*e.g.*, Hoskin *et al.* 2005), as on the other hand reinforcement by sexual selection can lead to rapid speciation under sympatric conditions, as shown for the radiation of the cricket *Laupala* on Hawaii (Shaw 2002, Shaw and Danley 2003, Mendelson and Shaw 2005). Today ecological speciation by adaptive divergence is increasingly viewed as a powerful engine of speciation, and is currently discussed as a key feature in particular of sympatric speciation.

Tests of ecological speciation include evidence for parallel evolution, *i.e.*, the development of the same phenotypic characters in closely related but independent lineages under identical extrinsic conditions (Schluter and Nagel 1995, Pigeon *et al.* 1997, McPeck and Wellborn 1998, Rundle *et al.* 2000, Mundy *et al.* 2004, Foster and Baker 2004, Colosimo *et al.* 2005), inverse correlations between morphological differentiation as an estimator of divergent selection and gene-flow as an estimator of reproductive isolation (Lu and Bernatchez 1999, Schluter 2000b), selection against hybrids (Rundle and Whitlock 2001), or assortative mating by selective environments (*e.g.*, Kondrashov and Shpak 1998, McKinnon *et al.* 2004, Seehausen *et al.* 2008). Recent models for speciation under divergent selection, comprising genetically differentiated and highly specialized populations of pea

aphids, were tested by Hawthorne and Via (2001) and Via and Hawthorne (2002). Another case study is presented in Sorenson *et al.* (2003). According to these recent views, speciation is considered a by-product of ecological differences under divergent selection on, often on only a small number of phenotypic and/or behavioral traits.

The current ecological context and natural as well as sexual selection can also be viewed as playing a decisive role in the diversification of species. Accordingly, as originally assumed implicitly by Darwin, natural selection and adaptation are the means of generating biodiversity, which is now also being discussed in context of adaptive radiations (see for reviews *e.g.*, Schluter 1996, 2000a, 2000b, 2001, 2009, Orr and Smith 1998, Sudhaus 2004, Rundle and Nosil 2005, Hendry *et al.* 2007, Patten 2008, Hendry 2009, Johannesson 2009, Nosil *et al.* 2009, Schluter 2009). Instead of geography, factors such as phenotypic plasticity, intra- and interspecific competition with character displacement and specialization as well as sexual selection lead to divergence and eventually to speciation. Thus, with ecology and selection discussed as a major player in the diversity of life, the underlying subject of allopatric versus sympatric speciation will remain a battleground in evolutionary biology for quite some time.

Hybridization and the genetics of speciation

In this context, the long debated phenomenon of interspecific hybridization, a major focus since the time of Darwin, has gained much attention lately (reviewed in Shaw and Danley 2003, Seehausen 2004, Mallet 2005, Noor and Feder 2006, Grant and Grant 2008, Schwenk *et al.* 2008, Presgraves and Yi 2009). Hybridization with introgression of alleles from one population into another is discussed as potentially enhancing adaptation, speciation and radiation, thus with potentially important consequences in evolutionary biology and speciation theory. Increasingly widespread phylogenetic evidence of cryptic introgression (even hybrid speciation at least in plants) is found in many groups, from Darwin's finches, cichlids and telmatherinid fishes to butterflies and sunflowers. An overview for hybridization is given in Coyne and Orr (2004), and recent discussion can be found in Seehausen (2004) and Mallet (2005), with case studies discussed in Glaubrecht (2010a). Using freshwater pachychilid gastropods of the genus *Brotia* H. Adams, 1866 from Thailand as examples of conflict between shell morphology and genetic diversity based on mitochondrial gene fragments (16S and COI) forming well differentiated haplotype lineages, Köhler and Deen (2010) have discussed evidence for introgression of mtDNA haplotypes, and considered hybridization between closely related species due to secondary contact the most likely cause.

Hybridization and introgression with varying levels of gene flow in the absence of strict allopatry are antagonistic to

the process of speciation, but, nevertheless, might play an important role in the context of adaptive radiation (*e.g.*, Seehausen 2004, Gavrillets and Losos 2009). While estimated to occur only in 10% of animal species, mostly young species, and thus found among closely related lineages, species flocks and adaptive radiations are most likely to provide suitable targets for studies, facilitated by modern molecular methods.

Diversification and adaptive radiation

Adaptive radiation explicitly links speciation and ecology. These two widely overlapping fields of research are arguably at the core of evolutionary biology. Thus, the study of adaptive radiation has the potential to significantly influence our perception of the living world in general. Radiations represent the most spectacular examples of the outcome of speciation processes. If assemblages of numerous closely related species endemic to a geographically confined area are addressed, the term species flock is usually employed (Mayr 1963). Species flocks are outstanding for their diversity and have attracted the interest of biologists ever since their discovery. Many have achieved textbook status as examples of explosive speciation and adaptive radiation, as the Darwin finches on Galapagos (Lack 1947, Grant 1986, Grant and Grant 2008), the Hawaiian drosophilids and crickets (Zimmermann 1958, Carson and Kaneshiro 1976, Shaw and Danley 2003, Mendelson and Shaw 2005), or the cichlid fishes in the East African lakes (Fryer and Iles 1972, Barlow 2000, Salzburger and Meyer 2004, Seehausen 2006) and the anole lizards in the Caribbean (Losos 2009). However, several other less spectacular flocks exist, also among molluscs, such as *e.g.*, the partulid snails on Pacific islands (Cowie 1992, Johnson *et al.* 1993) and gastropods in so called "ancient lakes", rendering islands as well as lakes as ideal natural laboratories (Glaubrecht 2010a, Wilke *et al.* 2010). The long-lived lakes, such as Lake Tanganyika, Lake Baikal, or the Malili lakes on Sulawesi (see below) are exceptionally rich in species numbers (Brooks 1950, Coulter 1991, Martens *et al.* 1994, Fryer 1996, Rossiter and Kawanabe 2000, Glaubrecht 2008a, Glaubrecht and Rintelen 2008a, Rintelen *et al.* 2010).

All these species flocks are regarded as examples of adaptive radiation, the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage, thus linking speciation and ecology (Schluter 1996, 2000a, 2000b, Glor 2010, Losos and Mahler 2010). Accordingly, three main processes are involved in radiations: (i) phenotypic divergence of natural populations driven by natural selection between environments, (ii) phenotypic divergence mediated by competition for resources, and (iii) ecological speciation. While some of these processes have been challenged, *e.g.*, competition and associated character displacement or the role of key innovations (Seehausen 2006), the concept of adaptive radiation has enjoyed wide recognition and interest

since the establishment of the modern synthesis. Within this framework, extrinsic factors such as major geographic changes provide the opportunity, and intrinsic factors such as key innovations in concert with adaptation and specialization provide the potential for radiation (Simpson 1953, Mayr 1963, Liem 1990, Schluter 2000b, Losos and Mahler 2010, but again see Seehausen 2006).

In conclusion we can say that the central controversy over models in speciation is far from being settled, as it is not yet resolved what genetic change will result in a new species and under which conditions, thus what the actual influence on speciation is of genetics, geography and adaptation to the environment. However, with new genetic research and genomic techniques homing in on the molecular and cellular mechanisms that enable diversification to occur, our current understanding of the speciation process and adaptive radiation has improved considerably. Eventually, this will provide answers to the next generation of questions on the frequency and importance of different processes that cause speciation.

MOLLUSCS IN SPECIATION STUDIES

"The most memorable lesson I learned from Darwin is that the most important thing in scientific research is not to add to the accumulation of facts, but to ask challenging questions about the how? and why? of biological phenomena and to try to answer them." Mayr (1999: 403)

The way in which speciation proceeds can only be fully understood by analyzing data collected from a large number of different model systems. To date, essentially only vertebrates are used (mostly birds and fishes, see above), while speciation mechanisms remain widely untested for many invertebrates, with the notable exception among insects, of butterflies, diptera and crickets. As evolutionary biologists working with molluscs, we should aim at testing the universality of known and disputed speciation mechanisms, and it is with a clear focus on these mechanisms we should choose our molluscan models to increase their frequency as a source of data in order to decipher the underlying mechanisms of biodiversity.

As was shown by Schwenk *et al.* (2008), mollusc species hold the same chance for studying evolutionary phenomena, in this case hybridization, as other groups. However, as noted before, *e.g.*, in case of the term "adaptive radiation" (Glaubrecht 2008b), too often malacologists use evolutionary biology issues for the titles of their papers or book section only, in lieu of a soundly designed study. As much as the term "adaptive radiation" is often misused, "speciation" not only reflects the taxonomic description of any speciose group, but instead the actual study of causation and underlying mechanisms of how species arise. Consequently, we should

not merely focus on the final stages of this process revealed in a fixed pattern, but actually attempt to study the complete process leading to a particular species assemblage. One symptomatic example for the ill-informed mis-use of the term "speciation" is Bandel's (2000) typological catalogue of chronospecies (at best, if at all distinct evolutionary entities) among the highly polymorphic fossil freshwater Melanopsidae. For a discussion of the over-naming of melanopsid forms and fossils see Glaubrecht (1993, 1996). Suffice it to state, as only one more example, Lazarus's (1983, 1995) attempts to deduce a sympatric mode of speciation from the microfossil record of pelagic protista such as foraminifera; other examples are discussed in Benton and Pearson (2001). From the debate among neontologists as to the paramount difficulties of distinguishing this particular mechanism from others (see above) we should at least have learned to meet such claims with much more reservation.

Instead of referring to "speciation" or "adaptive radiation" for each and every speciose taxonomic group we should strive to investigate, with adequate methods and founded on solid theoretical ground, the underlying mechanisms of anagenetic versus cladogenetic change. Then, certainly, molluscs can contribute to studying the highly interesting, yet controversial speciation mechanisms, hybridization and adaptive radiation. Not only freshwater snails (see below) and land snails (*e.g.*, Gittenberger 1988, Jordaens *et al.* 2009, to mention only very few here) but also marine gastropods have figured prominently in these investigations (Allmon and Smith 2011).

We still lack textbook examples of particular molluscs for sympatric and ecological speciation, adaptive divergence, and hybridization that are equally widely known let alone well studied, as provided among the vertebrates. Yet, there are suitable candidates among gastropods in ancient lakes, from oceanic islands and archipelagos, mountains or other insular environments with endemic species, as is evident from the contributions to a recent symposium on speciation in such environments (Glaubrecht 2010b).

Marine mollusc studies

For aquatic animals, in particular molluscs, the marine and limnic realm and their organisms are studied separately. For example, Bilton *et al.* (2001) and Bohonak and Jenkins (2003) discussed evolutionary ecological implications of speciation and dispersal in freshwater organisms, while Palumbi (1992, 1994, 1996) reviewed similar aspects including genetic divergence and reproductive isolation for marine organisms. In addition, the many detailed case studies on speciation mechanisms and on historical biogeography only look at one aquatic environment, largely ignoring taxa with amphidromous life history and habits that provide most elegant models for testing known hypotheses on speciation,

species diversity and range extension; for Cerithioidean gastropods see Glaubrecht (1996).

Recently, molecular genetic studies on various marine taxa have shown that the World's oceans are in fact not homogeneous areas as commonly held and that populations are much more structured in terms of their genetics than previously assumed. In many cases species ranges coincide with biogeographical boundaries as was shown for various gastropod taxa (*e.g.*, Hellberg 1998, Collin 2001, 2003, Williams *et al.* 2003, Williams and Reid 2004, Johannesson and André 2006, Reid *et al.* 2006, 2008, 2010, Lind *et al.* 2007, Duda *et al.* 2008, Malaquias and Reid 2009). To evaluate the various explanations, such as isolation by distance or stepping stone dispersal, recent studies compared biogeographical patterns and inferred a specific (in this case allopatric) mode of speciation in concert with vicariance, due to plate tectonics and in light of age estimates of the events (Williams and Reid 2004, Williamson and Duda 2008, Reid and Williams 2010). However, for most marine taxa the phylogenies have not been established sufficiently to allow detailed investigation on range expansion, with the aim of looking into correlation of potentially narrow range occurrences and speciation.

Hinting at the "marine paradox", *i.e.*, that marine species often have pelagic larvae and extensive geographical ranges in a seemingly homogeneous ocean, suppressing allopatric speciation, Allmon and Smith (2011) reviewed examples of speciation in (fossil) marine molluscs. Although it is expected to find an allopatric pattern and mechanism (see above, for a contrary view *e.g.*, Johannesson 2009), allopatry can have quite different causation, such as vicariance by tectonics or climatic and oceanographic factors as well as by dispersal across still existing geographic barriers. Sophisticated molecular phylogenetic studies and phylogeographic analyses are needed here for an evaluation of geological age and the exact mechanism of marine speciation. For more discussion on the phylogenetic approach, see below.

While the plethora of studies in this context essentially use phylogenetic and phylogeographic data to infer speciation mechanisms, only in very few cases are detailed analyses performed looking into the details of the causation for speciation. One example comes from a series of papers on the strongly polymorphic marine snail *Littorina saxatilis* (Olivi, 1792) studied by Johannesson (*e.g.*, 2001, 2009, see also Johannesson *et al.* 1995, Wilding *et al.* 2001, Johannesson and André 2006, Quesada *et al.* 2007) using parallels in populations of sympatric morphs and/or ecotypes with overlapping distributions and hybrids to suggest habitat selection, non-random (*i.e.*, assortative) mating and possibly sexual selection to not only contribute to, but maybe even cause sympatric reproductive isolation. However, we should not mistake such cases of parallel speciation as indicating only

sympatric divergence and sympatric speciation, as suggested by Johannesson (2001, 2009). Parallel speciation also occurs between allopatric populations and ecotypes that could once have arisen in allopatry and only later became sympatric (Schluter *et al.* 2001).

Freshwater molluscs

With respect to freshwater gastropods we are even further away from really understanding the details of species formation that leads to the array of radiations described for many taxa and cases. Again, speciation should not be understood as merely reflecting the compilation of species descriptions of any speciose group, as I have criticized above. More importantly, there are two main problems involved here: First, the difficulty still remains on the species level that molecular techniques in concert with lineage-based thinking have led to an increase (by an estimated 20 to 60%) in the number of what is called in these studies either "phylogenetic species" or "evolutionary significant units", often applied in avoiding to assess the status as distinct (bio-) species. This problem of overnaming, or taxonomic redundancy that in the past has caused the existing plethora of synonyms, in concert with the increased assignment of insufficiently differentiated subspecific populations to ("cryptic") species status, both lead to a taxonomic inflation that needs much more attention, as pointed out in Glaubrecht (2004, 2009). Glaubrecht *et al.* (2009) provide a case study among Australian freshwater thiarid gastropods. Only now, after more than a decade of the unhealthy spread of DNA barcoding, this approach is rightly criticized as being an anti-intellectual endeavour (see *e.g.*, reviews in Lee 2004, Meier 2008, Ebachs and Carvalho 2010).

Second, speciation is not to be understood as being revealed comprehensively by particular phylogenetic patterns since it is the result of a more complicated and continuous process. We need to realize more often that the cladograms, or "cloudograms" (as they have been more properly termed, Zachos 2009) resulting from sequence analyses of partial fragments of very few genes are far from being the best way to truly reflect details of the process of formation of species. Accordingly, these patterns only allow very limited inferences on the speciation process involved.

Thus, it is not surprising that we see a plethora of pattern-based studies with statements on lineage-base "species", but only few reliable insights into the underlying causation of speciation itself. Even for most speciose freshwater taxa, such as *e.g.*, the rissooidean *Bythinella* Moquin-Tandon, 1856 with wide species distribution in continental Europe (Bichain *et al.* 2007, Haase *et al.* 2007, Benke *et al.* 2009, Wilke *et al.* 2010), or hydrobiids in North America (Hershler *et al.* 2005, Hershler and Liu 2008), essentially only phylogenetic approaches and phylogeographical analyses are available. Most authors

struggle with the paramount problem of species delimitation without further exploring speciation mechanisms. This holds true, for example, for freshwater gastropods such as the Ancyliidae (e.g., Pfenninger *et al.* 2003, Walther *et al.* 2006) and Neritidae (Feher *et al.* 2009), with the genetic, ecological and morphological differentiation studied, or the Vivipariidae (Sengupta *et al.* 2009) and Ampullariidae (Haynes *et al.* 2009a, 2009b), with a focus again on aspects of global phylogeny and biodiversity. More examples, in particular among the lacustrine and riverine freshwater Cerithioidea, will be reviewed and discussed below.

Unfortunately, not only the fossil record (see below) but also standard molecular phylogenetic analyses (in particular when using mtDNA gene fragments such as the bar coding gene COI) often lack the temporal and spatial resolution to allow any more detailed inferences on speciation modes. Being either explicitly or implicitly aware of this, only very few studies claimed evidence for incipient speciation in aquatic snails, albeit deduced merely from a gene tree (e.g., Colgan and Ponder 2000). Other studies decisively ruled out the otherwise often implicitly suggested hypothesis of so-called “cryptic speciation” when finding large COI divergences (e.g., Walther *et al.* 2006). However, to date none of these studies (with the exception of those in “natural laboratories”, see below) are experimentally designed and/or conducted to actually allow for detailed insights into how exactly species multiply in molluscs.

One of the urgent questions to answer is, for example, how far different modes of speciation contribute to the diversity among and within particular taxa. Deduced from a given phylogenetic pattern more often than not an allopatric setting is assumed, while a discussion of other, e.g., ecological factors, is largely lacking. In this context, an integrative evolutionary ecology approach has been suggested, aiming to reconstruct the origin and alteration of the ecological interrelations of organisms and their respective environments in the course of evolution, as defined and explained in more detail by Glaubrecht (1996). This approach provides a research program for acquiring a synthetical perspective that includes morphology, molecular genetics, ecology and biogeography, in order to look into the speciation process beyond the point where we simply assume geographical factors (allopatry). Bilton *et al.* (2001) and Bohonak and Jenkins (2003) reviewed some of the evolutionary ecology implications in freshwater organisms in general, while Glaubrecht (1996, 2000) has discussed these for limnic groups among the Cerithioidea.

One central aspect in this context is, of course, the question of dispersal and colonization ability, thus gene flow and genetic divergence, of taxa that are highly restricted by their essentially patchy habitat. Since active as well as passive dispersion can rarely be investigated directly, inferences have

to be made via mostly molecular markers. Depending on the taxon and occurrence, the habitat conditions, e.g., drainage system, lacustrine constellation, and geographic isolation, have to be considered in concert with intrinsic biological properties. However, these are only rarely studied (Bilton *et al.* 2001). The review of Bohonak and Jenkins (2003) discloses how far away we are from a thorough understanding of the evolutionary ecology of freshwater gastropods, truly integrating knowledge on dispersal, gene flow, life history into a phylogenetic and phylogeographic framework. As we lack any more detailed studies as well as verification and general theory on this, some authors (Harvey 2002, Ponder and Colgan 2002) have simply claimed that among freshwater molluscs so-called “narrow range” taxa (*i.e.*, those with restricted occurrences) tend to speciate more. Similar claims that, for example, viviparous taxa among limnic gastropods are generally not only more restricted as to their distribution but also, as a rule, more speciation-prone (e.g., Michel *et al.* 1992, 2004, Michel 1994, 2000) have been shown to be essentially unsupported by evidence (see, e.g., discussion in Glaubrecht 1996, 1999, 2006).

How much malacology contributes to important issues in evolutionary biology and speciation in particular can be seen from the review and papers given during the World Congress of Malacology 2007 in Antwerp, and its resulting publications (see Glaubrecht and Rintelen 2009 and references therein), as well as from the present volume (Allmon and Smith 2011). Further details will be given for those cases which I discuss below for studies on limnic lineages among the Cerithioidea (Fig. 1).

PATTERN AND PROCESS OF SPECIATION IN CERITHIOIDEA: EMPIRICAL APPROACHES

“One lesson to consider is that when theoretical frameworks are lost, empirical information disappears with them.” Nyhart (2002: 12)

Unfortunately, malacologists felt that describing any assemblage of species (names) of living or fossil taxa as well as analyzing alignments of partial gene fragments with standard algorithms already justifies the attribute of any kind of speciation study. With respect to our “Darwinian mysteries”, or the big questions for the near future of biological sciences (see Glaubrecht 2009), though, the subject of speciation is more complicated than reflected in these simplistic approaches.

First, we need to realise one misleading aspect of supposedly “modern” biodiversity research. Our yet unresolved questions concerning species numbers, species concepts and speciation go well beyond those aspects covered by the many current biodiversity inventory projects. Sadly, these are

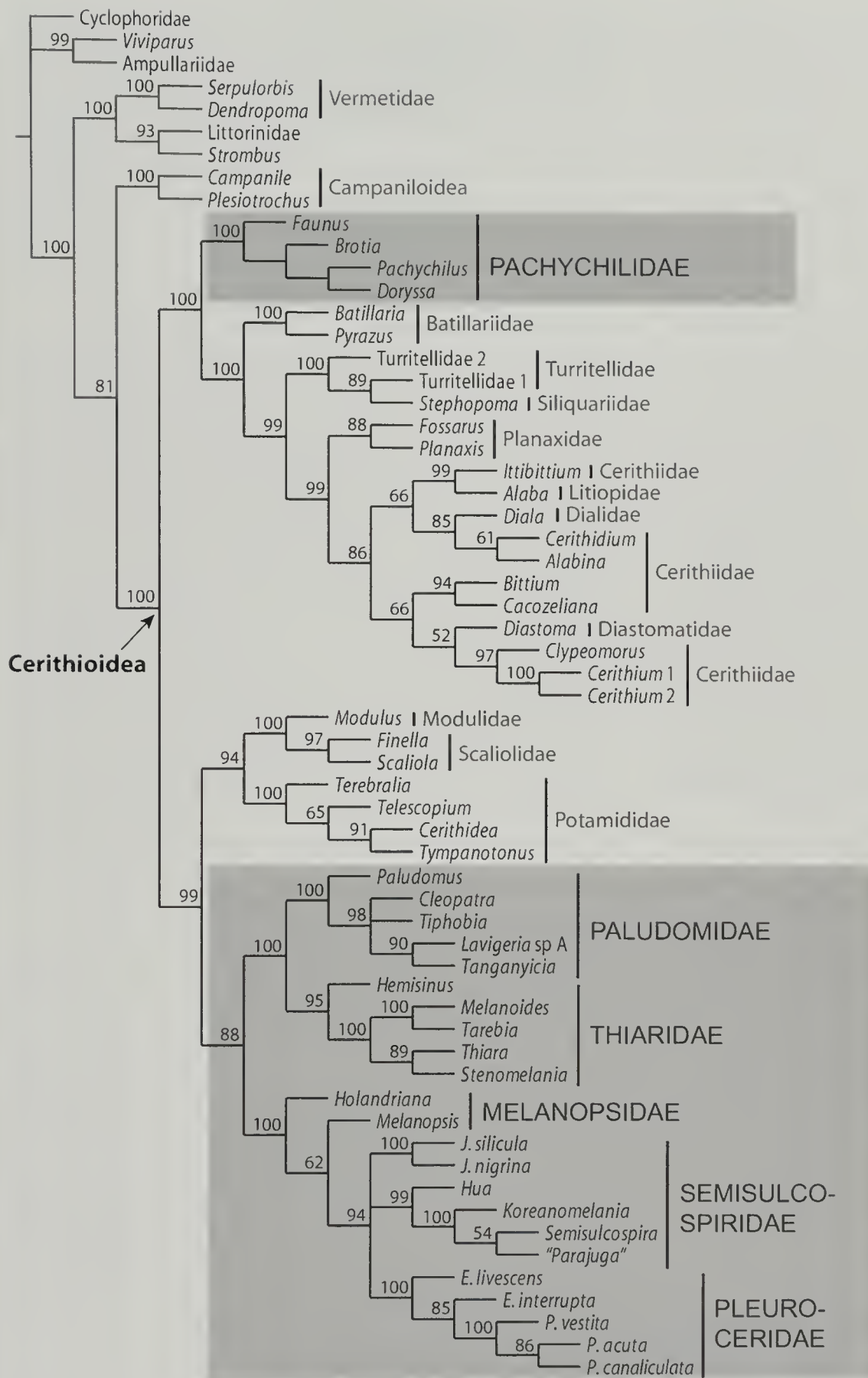


Figure 1. Cladogram of the caenogastropod superfamily Cerithioidea, based on the Bayesian analysis of a combined morphological and molecular dataset (16S, 28S, with unconserved regions removed), modified from Strong *et al.* (2011). Freshwater lineages are highlighted.

limited to simply cataloging and inventoring all given names or taxa of an area, rather than attempting to face the paramount problems with species definitions and delimitations, synonymy and taxonomy redundancy, or any understanding of forces that ultimately result in the patterns found. We yet have to resolve, for example, whether species richness is a reliable proxy of (accelerated) speciation and whether any species assemblage or flock is a proxy of any particular mechanism of speciation.

Second, as we have seen above, inferences from geographic patterns have dominated the literature, together with the study of allopatric speciation (e.g., Mayr 1942, 1963). Many molecular phylogenies and in particular phylogeographic studies are now available (Hickerson *et al.* 2010); for aquatic molluscs see Wares and Turner (2003). However, our interpretation of phylogenetic as well as biogeographic patterns largely depends on our concepts of the modes of speciation and cladogenesis in general, as was rightly pointed out by Heads (2009), although he only discussed dispersal versus vicariance, and a new method of analyzing the biogeography of a given group. While the statistical rigor of the new discipline of phylogeography has increased, and an ambitious synthesis is envisioned (Hickerson *et al.* 2010), we still lack deeper insights into the mechanisms of speciation. While Barraclough and Vogler (2000) have suggested how to investigate the role of speciation from species-level phylogenies, Losos and Glor (2003) remained sceptical and have even proposed that inter-specific phylogenies are unable to test alternative hypotheses of speciation, for example the role of geology and the adaptive process.

Irrespective of this criticism and discussion, we currently employ three empirical approaches in the study of speciation:

- (i) the phylogenetic comparative method, *i.e.*, looking into pattern of molecular phylogenies,
- (ii) fossils, *i.e.*, inferring the history of a clade through time, and
- (iii) microevolutionary studies of extant taxa, with focussing on traits and processes.

Contrasting lacustrine with riverine settings, I discuss these issues here exemplified by our studies on several pantropically distributed limnic Cerithioidean gastropod taxa (Fig. 1), which range from the New World and the Mediterranean region to lakes and rivers in East Africa and SE Asia to Australia. A taxon-by-region overview of the six distinct phylogenetic lineages of freshwater Cerithioidea currently considered on the family level is presented in Table 1. It should be noted that these six families were traditionally considered as “Melaniidae” until only a few decades ago, and that several of these distinct lineages were then for long subsumed under Thiaridae. However, our phylogenetic analyses of constituent groups as well as within the Cerithioidea context (reviewed in Glaubrecht 1996, 1999, 2006, Lydeard *et al.* 2002, Strong *et al.* 2011) have revealed the existence of two (or potentially three) independent lineages that probably colonized freshwater since the Mesozoic (Fig. 1).

It is in the context of speciation and radiation that these freshwater Cerithioidea have recently been described as truly “Darwinian snails”, based on studies on paludomid snails in East Africa’s Lake Tanganyika (Glaubrecht 2008a), the freshwater pachychilid *Tylomelania* Sarasin and Sarasin, 1897

endemic to rivers and central lakes on the Indonesian island of Sulawesi (Glaubrecht and Rintelen 2008a, Rintelen *et al.* 2010), two endemic riverine *Pseudopotamis* Martens, 1894 on the Torres Strait Islands (Glaubrecht and Rintelen 2003), *Brotia* in rivers in central Thailand (Glaubrecht and Köhler 2004, Köhler *et al.* 2010), and the riverine *Madagasikara* Köhler and Glaubrecht, 2010 on Madagascar (Köhler and Glaubrecht 2010).

Phylogenetic comparative method: patterns of molecular phylogenies

With an increasing armamentarium of molecular genetic techniques for exploring the genetic structure of populations, species and higher level taxa, the one mystery of how species originate has become many, and possible solutions multiplied. Not only have we uncovered further complexities in what we mean by species, but we also gained further insights into the drivers and rate of speciation. However, molecular systematists realize now that cladograms are actually more like “cloudograms”. Gene fragments reflect gene genealogies, or molecular “gene trees”, but are not identical to organismic phylogenies, or “species trees”, a fact that was pointed out early by Maddison (1997). The lack of identity is explained, among other causes, as due to the coalescent process of species divergence, resulting over time from genetic drift and incomplete lineage sorting (*i.e.*, the maintenance of an ancestral allele polymorphism across population or species boundaries with the coalescence process not completed for

Table 1. The biogeography of freshwater Cerithioidea taxa, listed by family, on a global scale. The six families, with their constituent taxa, as currently conceived, are given here as delimited in Glaubrecht (1996, 1999, 2006), Glaubrecht and Rintelen (2008b), and the most recent overall phylogenetic analysis in Strong *et al.* (2011). For species-level classification see references listed in the footnotes.

Region	America / Caribbean	Europe / Palaearctic	Africa	Asia	Australia / NZ
taxon	Pachychilidae Pleuroceridae ⁴ Semisulcospiridae ⁵	Melanopsidae ⁷	Pachychilidae ¹ Paludomidae ⁹ Thiaridae ⁹	Pachychilidae ² Semisulcospiridae ⁶ Paludomidae Thiaridae ¹¹	Pachychilidae ³ Melanopsidae ⁸ Thiaridae ¹²
	Thiaridae ¹⁰				

¹ With *Potadoma* on continental Africa and *Madagasikara* endemic to Madagascar, see Köhler and Glaubrecht (2010)
² Köhler and Glaubrecht (2001, 2003, 2006, 2007), Köhler and Dames (2009), Rintelen *et al.* (2007)
³ With only two species of *Pseudopotamis* endemic to the Torres Strait Islands, see Glaubrecht and Rintelen (2003)
⁴ Restricted to North America, for phylogenetic analysis see Holznagel and Lydeard (2000) and Strong and Köhler (2009)
⁵ Restricted with *Juga* to the western drainages in North America, see Holznagel and Lydeard (2000) and Strong and Köhler (2009)
⁶ Restricted to Far East Russia, Japan, and Korea, for phylogenetic analysis see Strong and Köhler (2009)
⁷ Glaubrecht (1993, 1996)
⁸ With few melanopsid species restricted to New Caledonia and New Zealand only, see Glaubrecht (1996)
⁹ Wilson *et al.* (2004), Glaubrecht (2008a), Glaubrecht and Rintelen (2008b)
¹⁰ With Hemisininae on Caribbean islands and mainland South America only, Glaubrecht and Rintelen (2008b)
¹¹ Glaubrecht (1996, 1999, 2006), Glaubrecht and Rintelen (2008b)
¹² Glaubrecht *et al.* (2009)

the respective gene), or from hybridization. In addition, molecular geneticists have repeatedly discussed necessary optimization and shortcomings of mtDNA sequence data in phylogeography and molecular ecology (Avice 2000, 2006, Whelan and Goldman 2001, Funk and Omland 2003, Lee 2004, Meier 2008). Not only is species-level paraphyly and polyphyly far more common (up to 23% of studied taxa) than generally recognized, calling for careful interpretation of species limits and speciation phenomena, but the ignorance of the discordance of gene and species trees is widespread. Many authors take the results of their single-locus studies at face value, as discussed in Zachos (2009), producing highly unsatisfying taxonomies.

Accordingly, phenomena such as coalescence and processes such as incomplete lineage sorting need to be taken into account in systematics and evolutionary biology to avoid erroneous conclusions. We need to realize that gene trees resulting from many of our recent (phylo) genetic studies are at best “weak null hypotheses of population relationships” (Dillon, pers. comm., 2008), allowing only poor inference regarding the actual evolutionary relationship between species. I will hint at only a few examples where this holds true in freshwater gastropods (e.g., Walther *et al.* 2006, Sengupta *et al.* 2009) and among the Cerithioidea in Pachychilidae (Rintelen and Glaubrecht 2002, Glaubrecht and Köhler 2004, Köhler and Glaubrecht 2006, Köhler and Dames 2009, Köhler and Deen 2010, Köhler *et al.* 2010, Rintelen *et al.* 2010) and in Pleuroceridae (e.g., Dillon and Frankis 2004, Lee *et al.* 2007, Dillon and Robinson 2009).

Nevertheless, molecular species-level phylogenies and the comparative method still allow certain insights into the origin of diversity by speciation and radiation, albeit mostly without explicit inference of the exact mechanisms. For example, two of our own studies on brackish-water Cerithioidea revealed interesting patterns as to the presence of more speciose clades among species-poor or even monotypic genera within the Potamididae (Reid *et al.* 2008) and the Batillariidae (Ozawa *et al.* 2009), both common in the Indo West-Pacific. In potamidids we correlated the origin of the 29 living species with a speciation event in the Tethyan realm in the Middle Eocene, and the appearance of mangrove habitats on which they still depend today, thus suggesting that potamidids in fact do represent an adaptive radiation and have always been closely associated with mangroves. We also found the 14 living batillariid species to represent a Tethyan relict, reaching Australasia by the Late Oligocene, with four genera still surviving in this refugium. Only within one lineage, *Batillaria* Benson, 1842 that started to migrate north in the Early Miocene, our phylogenetic analyses revealed a radiation into eight species. The remaining genera are species-poor if not even monotypic.

Of course, those patterns are interesting in themselves as they help to establish the phylogenetic framework. Applying phylogenetic methods yields patterns of genetic affinity that allow us to judge past events of divergence. Nevertheless, the comparative method only provides a first indication for speciation under the influence of either geographical or ecological factors, pointing out future avenues towards a truly evolutionary ecology approach. We are far away from this goal with respect to the phylogeny and phylogeography of freshwater cerithioidean families such as the Pachychilidae (Köhler and Dames 2009, Köhler and Glaubrecht 2010), the Paludomidae (Wilson *et al.* 2004), Semisulcospiridae (Strong and Köhler 2009), the Melanopsidae and Thiaridae (Glaubrecht and Rintelen, unpubl. data) as well as the Pleuroceridae (Glaubrecht and Köhler, unpubl. data).

Fossils: inferring history of clades through time—case study from Lake Turkana

“Paleontology is the historical science that weaves historical narratives around evolving species.” Hull (1989: 186)

The fossil record provides not only a wonderful but the only direct documentation of events in the history of evolution. The discipline has seen a revolution over the last few decades (Sepkoski and Ruse 2009), and speciation has been at the forefront of modern paleontological theory since Eldredge and Gould (1972) first proposed their theory of “punctuated equilibrium”, a model for discontinuous tempos of change in the process of speciation and the deployment of species in geological time. Since then, improved approaches to speciation in the fossil record have been claimed (e.g., Erwin and Anstey 1995) and speciation modes and case studies reviewed (e.g., Allmon 1992, Gould and Eldredge 1993, Benton and Pearson 2001, Hendry 2008, Allmon and Smith 2011). In this context, stratigraphic resolution and acuity are of paramount importance. As high-resolution, stratigraphic sequences with appropriate time controls are generally rare or lacking in most formations and fossil strata, confirmation of speciation has been difficult to find in fossils. Nevertheless, in rare cases it is possible to infer evolutionary processes, including even adaptation by natural selection and the formation of new speciation from temporal patterns in phenotypic traits, such as size, shape or sculpture in molluscs. These patterns are, for example, consistent directional trends, constancy (or stasis) and randomness. See Hendry (2008) for discussion of an exemplary fossil sequence in sticklebacks from an ancient lake.

Undoubtedly, for the fossil record of freshwater gastropods, Williamson’s (1981, 1985) claim of having found evidence for speciation and punctuated equilibrium in Plio-Pleistocene molluscs of the East African Turkana formation is still the most famous, albeit also highly controversial one. Next to bivalves (which are not considered here), the

most abundant fossil gastropods found in the Lake Turkana beds spanning 2 my belong to the two Cerithioidean families Paludomidae (*Cleopatra* Troschel, 1857) and Thiaridae (*Melanoides* Olivier, 1804). Starting with Williamson until recently these were confused as both being thiarids with the same biological properties, such as *e.g.*, reproductive mode. However, the widely distributed paludomids in Africa are oviparous and gonochoristic (with exceptions discussed in Glaubrecht 2008a, 2010c, Glaubrecht and Strong 2007), while all thiarids are viviparous with a sub-hemocoelic brood pouch and, additionally, with *Melanoides* also being parthenogenetic (Glaubrecht 1996). In addition, to control for stratigraphy, these differences in life history of the Turkana molluscs are crucial for the interpretation in context with the claim of speciation in general and of evolutionary modes involved in particular.

Williamson (1981, 1985) described peculiar morphological changes in the “iconic” gastropods, attributing it to radiation under the punctuated equilibrium theory and (sympatric) speciation pulses followed by extinction of the, curiously enough, new species. Critics doubted this change being evidence for speciation and radiation in the fossil record, and alternatively suggested he merely documented ecophenotypical responses to environmental changes under stress. For a review of the debate see Williamson (1985) and Glaubrecht (1996: 140-142, 373-378, and references therein).

It is important to take into account that, of all thiarids known, in particular *Melanoides tuberculata* O. F. Müller, 1774 is phenotypically highly plastic in several shell traits. Nevertheless, changes in shell morphology in this and other molluscs can indeed be correlated to facies changes which we re-considered within a revised stratigraphic framework. Our own ongoing study of the Turkana molluscs revealed that they actually provide one of the rare cases of high-resolution stratigraphic sequences with appropriate time controls. Re-studying the time sequence of *Melanoides tuberculata* and *Cleopatra ferruginea* I. Lea and H. C. Lea, 1850 from the original material in the Williamson Collection, Museum of Comparative Zoology at the Harvard University, as well as our own collections done in 2006 and 2010 at Turkana, allowed us to reconstruct faunal successions instead of speciation. For preliminary results see Scholz and Glaubrecht (2007), Glaubrecht *et al.* (2009) and Scholz *et al.* (2009); a detailed account will be published elsewhere. As illustrated in Fig. 2 for one exemplary part of the Turkana record, normalized and intermediate *Melanoides* morphs are found to succeed each other, later being replaced by small, needle-like morphs. These latter phenotypes resemble salinity-stressed recent *M. tuberculata* living in coastal lagoons and brackish creeks (Glaubrecht, unpubl. data).

In contrast to Williamson’s earlier hypothesis, but in concurrence with recent stratigraphic and sedimentological

studies (Craig Feibel and Henning Scholz, unpubl. data), morphological change in *Melanoides* has to be viewed as being gradual, while only few abrupt changes are associated with pronounced alterations in facies or sedimentological interruptions. Accordingly, we propose that fluctuating environments in the region of the Turkana paleo-lakes triggered the observed morphological variation in gastropod shells, leading to the repeated extinction of lacustrine populations and later immigration of riverine populations into paleo Lake Turkana, mimicking punctuated equilibrium with stasis and sudden bursts of radiation (Scholz and Glaubrecht 2007, Glaubrecht *et al.* 2009, Scholz *et al.* 2009). Although we found support for Williamson’s original description of highly resolved morphological change through time, his interpretation of rapid bursts of (punctuated) evolutionary change has to be replaced by the alternative that these changes documented in the fossil record resulted from the invasion of extra-basinal, con-specific populations. Therefore, the Turkana gastropods (and most likely other molluscs as well) do not provide a case study for the theory of punctuated equilibrium and no documentation of speciation events in fossils.

Microevolutionary studies of extant taxa: focussing on traits and processes

“If there is the slightest foundation for these remarks, the zoology of Archipelagos will be well worth examining; for such facts [would] undermine the [theory of the] stability of Species.” Darwin 1836 (in Barlow 1963: 201)

While speciation occurs faster than generally observable in the (punctuated) fossil record, evolutionary events are considered too slow for study on biological timescales. Long before Georg Evelyn Hutinchson (1965) hinted at the ongoing “evolutionary play” in the “ecological theatre” of lakes as microcosms, Charles Darwin’s son, Francis Darwin (1909: xii, 26) first mentioned the Galapagos islands “as a microcosm of evolution”. In this tradition and given our focus on speciation and radiation, we consider oceanic islands and inland lakes as equally well-suited microcosms for exemplary microevolutionary studies. The rise of molecular genetics and its rapid application in phylogenetic systematics has produced over the last two decades new phylogenies for classical cases of adaptive radiation, such as the Galapagos finches, but also phylogenies for new model systems, such as the cichlids of lakes in the Neotropics and Africa (see above) as well as our limnic molluscs.

Much has been written on species flocks in particular in “ancient” or long-lived lakes, which have featured prominently in evolutionary biology, often regarding these evolutionary theatres also as hotspots of diversification, as they are exceptionally rich in species. As well as their fish radiations, ancient lakes such as Lake Tanganyika, Lake Malawi, Lake Baikal and Lake Biwa also harbor one or more

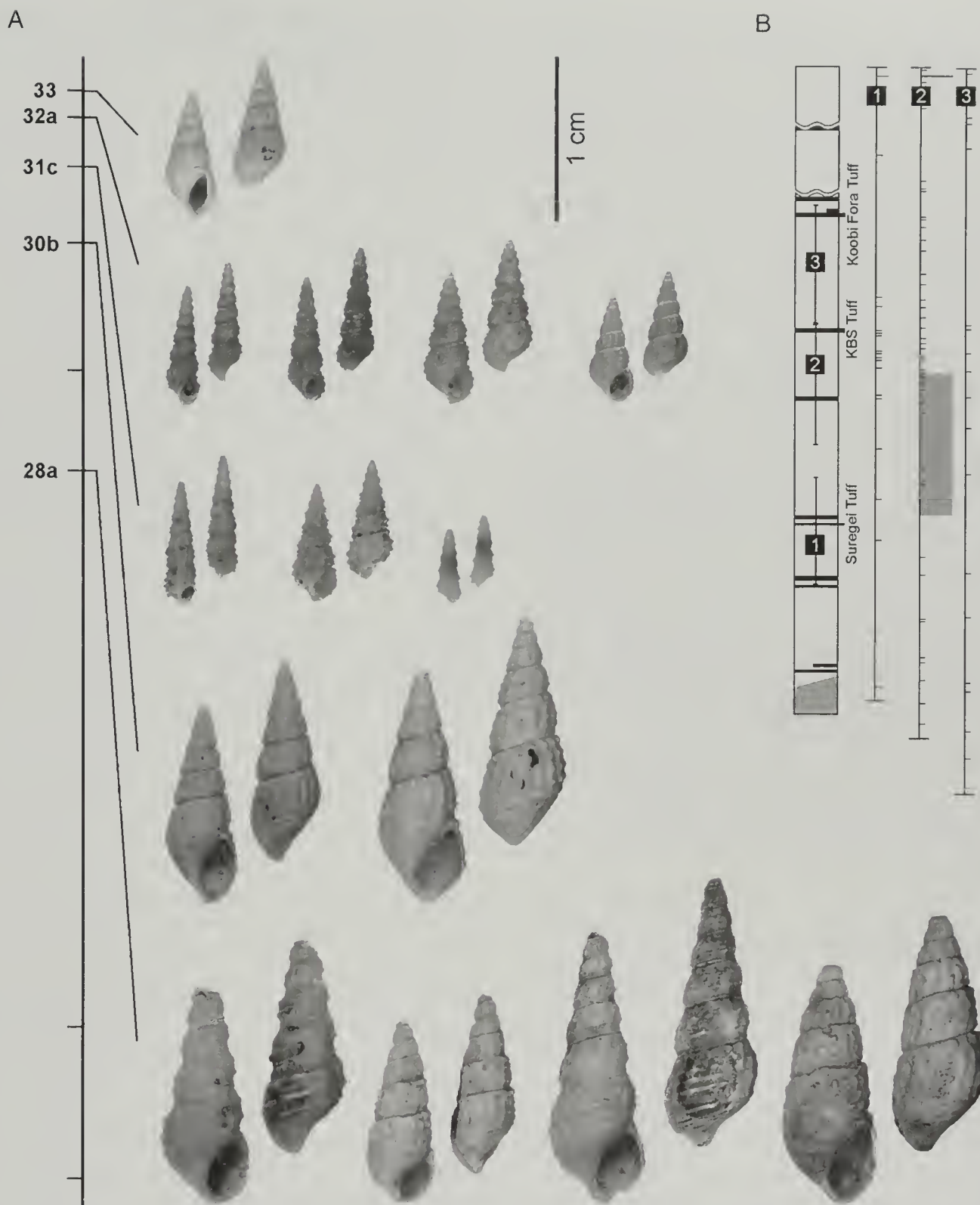


Figure 2. A, Reconstruction of a partial section of the faunal succession in *Melanoides tuberculata*, a thiarid gastropod from the Plio-Pleistocene Koobi Fora Formation in the eastern Turkana Basin of East Africa. Typical representatives of mollusc faunas from the original Williamson Collection, numbered from 28a to 33. Note the appearance of needle-like forms from fauna 31c onwards, with the morphological variability being higher and shell size much smaller than in older and younger strata. B, The composite stratigraphic column and divisions of the Turkana Basin deposits with stratigraphical distribution of the mollusc faunas, modified from Williamson (1981). The shaded area marks the partial section shown in A.

invertebrate species flocks of gastropods, bivalves, crabs and shrimps (examples and reviews *e.g.*, in Brooks 1950, Boss 1978, Coulter 1991, Fryer 1991, 1996, Martens 1994, Rossiter

and Kawanabe 2000, Wilke *et al.* 2008, Glaubrecht 2010). Derived with modern methods, new molecular phylogenies have challenged older ideas about the age and origin of these

species flocks, while offering opportunities to rigorously test hypotheses on modes of speciation, divergence times, character evolution and adaptation.

I focus on the gastropods from two of these ancient lakes as well as some rivers, since both settings provide ideal model systems to study speciation processes with respect to morphological, molecular genetic, geographical and ecological aspects. In particular, the (presumptive) endemic evolution of a gastropod species flock in the East African Lake Tanganyika, as well as that in central lakes on Sulawesi, Indonesia, provide instructive comparative case studies of speciation and radiation. In contrast, riverine radiations are both rarely known and less well studied. Although making up less than 1% of the world’s water, running freshwater, or lotic systems, are more permanent on both ecological and evolutionary timescales than most lakes, or lentic habitats. Thus, fluviatile radiations make an interesting contrast to known lacustrine radiations, since they allow us to judge the

decisive role of the environment (riverine versus lacustrine setting) in speciation modes, *i.e.*, allopatric versus ecological speciation (Table 2).

Species flocks in ancient lakes—Cerithioidean gastropods as models

Irrespective of being suitable model systems, our knowledge on the taxonomy, systematics and evolution of several snail species flocks in ancient lakes remained rudimentary for long. Members of these radiations possess unique morphologies very different from those of their riverine relatives, and display a wide array of phenotypic and ecological diversity, as illustrated by Lake Tanganyika gastropods (Glaubrecht 2008a) and the Sulawesi lakes (Glaubrecht and Rintelen 2008). Interestingly, as a rule no riverine species are found in these lakes and *vice versa*. Two hypotheses have been put forward to explain the different shell morphologies of lake and riverine species: escalation

Table 2. Evaluation of speciation and adaptive radiation in freshwater Cerithioidean gastropods from lacustrine and riverine settings, applying the four formal criteria suggested by Schluter (2000a). For details and explanation see text. +, verification by the study cited below; -, lack of this criterion; ?, lack of respective data.

	Phylogenetic criteria:		Ecological criteria:	
	Common ancestry	Rapid speciation	Phenotype-environment correlation	Trait utility
Lacustrine setting:				
- Paludomidae thalassoid species, Lake Tanganyika	+ / + ¹ (Wilson <i>et al.</i> 2004, Glaubrecht and Strong 2007)	+ ²	?	?
- Pachychilidae <i>Tylomelania</i> , central Lakes on Sulawesi	+ ³ (Rintelen <i>et al.</i> 2004, 2007, 2010)	+	+	?
Riverine setting:				
- Paludomidae <i>Potadomoides</i> , Congo River system	+ (Glaubrecht and Strong 2007)	?	?	?
- Pachychilidae <i>Pseudopotamis</i> on Torres Strait Islands	+ (Glaubrecht and Rintelen 2003)	-	-	?
<i>Tylomelania</i> on Sulawesi	+ (Rintelen <i>et al.</i> 2004, 2007)	- (+ ⁴)	- / + ⁴	?
<i>Brotia</i> , Kaek River in Thailand	+ (Glaubrecht and Köhler 2004)	+	+ / ? ⁵	?
<i>Madagasikara</i> on Madagascar	+ (Köhler and Glaubrecht 2010)	-	-	?

¹ Note that Glaubrecht and Strong (2007) and Glaubrecht (2008a) concluded independent colonization events in the paludomids of this lake, suggesting the existence of at least two distinct species flocks within the lake. Nevertheless, both have been found as closely related within the monophyletic African paludomids.

² Note that only in case of *Lavigeria* rapid speciation is likely. See Wilson *et al.* (2004) for details on the phylogeny.

³ Note that within the endemic *Tylomelania* there is evidence for four independent monophyletic clades having colonized the lake systems.

⁴ Only verified so far for the case of three syntopic species in the Balocci Valley, SW Sulawesi (Rintelen *et al.* 2007).

⁵ Note that Köhler *et al.* (2010) verified common ancestry and rapid speciation, but not phenotype-environment correlation.

(see review in Glaubrecht 1996) versus neutralism without any role of adaptation (Gorthner 1992). Escalation, *i.e.*, predator-prey coevolution, has been positively tested for crabs and snails in Lake Tanganyika (West *et al.* 1991, West and Cohen 1994, 1996) and in the Malili lakes on Sulawesi (Rintelen *et al.* 2004).

For a long time, intralacustrine geographical separation, as a version of (micro-)allopatric speciation, was the generally assumed (though rarely explicitly stated) null hypothesis for the origin of the diversity within a lake. On the other hand, any test of the involvement of natural selection and adaptation, *i.e.*, an ecological component to speciation, was essentially lacking. According to the ecological theory of adaptive radiation (Schluter 1996, 2000a, 2000b, 2001), species flocks are the outcome of divergent natural selection resulting from resource competition (see the first section of this paper for more details). Thus, although the concept of adaptive radiation has enjoyed wide recognition and interest, most alleged cases, and even textbook examples of adaptive radiation were hardly tested with good models.

Only recently has the definition of adaptive radiation been rigorously translated into formal criteria (Schluter 2000a). Accordingly, the two principal components of adaptive radiation are rapid, multiple splitting of a lineage (speciation) and the origin of new ecological and phenotypic forms in each speciation event. For these components Schluter (2000a) proposed four criteria, which should be tested to confirm that the system under consideration indeed represents an adaptive radiation: (1) monophyly (or common ancestry), (2) rapid speciation, (3) phenotype-environment correlation, and (4) trait utility; these provide two phylogenetic and ecological criteria each (see Table 2).

While the latter two criteria are most frequently neglected, and in particular, trait utility is extremely difficult to test even in well-known systems, the first two criteria are more readily testable today, but have not been applied rigorously in many cases yet. As speciation and adaptive radiation is widely considered to be one of the most important processes in evolution, this lack of basic data for most potential candidates is a major obstacle for our understanding of some of the most intriguing evolutionary phenomena. I review and have compiled in Table 2, for freshwater Cerithioidean model systems, the available studies, their results and implications, aiming at explicitly evaluating Schluter's four criteria for speciation and radiation.

Lake Tanganyika: The "thalassoid" species flock in paludomids

The thalassoid, *i.e.*, marine-like, Cerithioidean gastropods in East African's Lake Tanganyika provide one of the iconic examples of a spectacular endemic radiation. Although characteristic of the fauna of this Rift lake, the species flock long remained enigmatic with respect to its origin and

evolutionary history of its constituent members, as reviewed in Glaubrecht (2008a). Evaluating Schluter's criteria, I will focus on the monophyly of the entire Tanganyikan species flock and its potential riverine ancestry, as well as the speciation mode and aspects (Table 2).

Common ancestry

All former studies (Michel *et al.* 1992, 2004, Michel 1994, 2000, West and Michel 2000) have assumed (i) that these gastropods are Thiaridae, and (ii) an *in situ* radiation within Lake Tanganyika, explicitly or implicitly hypothesizing that the riverine *Potadomoides* Leloup, 1953 from the Congo River drainage is ancestral to the entire Tanganyikan radiation. In contrast, Glaubrecht (2008a) and Glaubrecht and Strong (2007) have shown based on morphological and molecular phylogenetic evidence (see also Wilson *et al.* 2004) both from the lake radiation itself and a study of the taxa in adjacent river systems, that (i) the thalassoid species in Lake Tanganyika are Paludomidae instead of Thiaridae (Table 1), (ii) that the lake most likely provides an evolutionary reservoir for several ancient confamilial African lineages, and (iii) that the uterine brooder *Potadomoides* represents the adelphotaxon to only the uterine brooder *Lavigeria* Bourguignat, 1888 (plus the oviparous *Vinundu* Michel, 2004), but not the entire essentially oviparous thalassoid species flock. Based on our phylogenetic analyses, we anticipate that the widely distributed paludomid *Cleopatra* most likely represents the sister taxon to most if not all the remaining thalassoid species in Lake Tanganyika.

Rapid speciation

Accordingly, at least two separate paludomid lineages have once independently colonized Proto-Lake Tanganyika, with only *Lavigeria* exhibiting subsequent radiation and increased speciation events within the lake, whereas most other thalassoid taxa are species-poor or even monotypic (Glaubrecht 2008a). While West and Michel (2000) suggested an "explosive origin" of the entire thalassoid gastropod radiation, we found in our phylogenetic analyses only in the case of *Lavigeria* evidence hinting at rapid speciation (Wilson *et al.* 2004); see Table 2. The viviparous *Lavigeria* has repeatedly been discussed as being especially prone to speciation, assuming that brooders have highly isolated populations more likely to diverge genetically and, thus, to eventually speciate (*e.g.*, Michel *et al.* 1992, Michel 1994). As much as this may or may not be true in general, it is difficult to confirm in the case of the thalassoid gastropods and *Lavigeria* in particular, since essential data on chorology (occurrence, range, and dispersal) and population genetics of the various morphospecies currently differentiated and/or re-erected from former Bourguignat's names by Michel and co-workers are available to only a limited degree (see discussion in Glaubrecht 2008a).

Ecology

Unfortunately, as the taxonomy and systematics of the latter genus has not yet been formalized, we lack sufficient morphological and/or ecological data to allow sound judgement on the question of trophic specialization or other differential adaptation under natural selection of individual taxa of this species flock. In several *Lavigeria* species, conchological congruence with substratum type and specific habitat preferences seems to occur, as reviewed in Glaubrecht (2008a). For example, it was hypothesized that rock-dwellers might be more subject to barriers to dispersal and eventually speciate (Michel *et al.* 1992, Michel 1994). However, to date we can only speculate that specific adaptations in *Lavigeria* could have played a role in intralacustrine speciation and adaptive radiation. In contrast to our studies on *Tylomelania* on Sulawesi (see below), we lack sufficient reliable data on specific radula morphologies and trophic specialization in *Lavigeria* being correlated with specific habitat and/or even food preferences.

Therefore, we find again in the case of Tanganyikan paludomids that the molecular genetic approaches have helped to resolve at least the basic patterns of genealogical relationships and ancestry (phylogenetic criteria, see Table 2). However, we still lack insight into the details of the species flock's geography and in particular ecology, as an explicit study on patterns and mode of speciation has not been undertaken yet. To date it remains equally likely that speciation in Lake Tanganyikan paludomids is promoted either by intralacustrine geography along the inshore environments inhabited by *Lavigeria* and other thalassoid snails, or by adaptation to ecological factors and other selective forces.

Central lakes, Sulawesi: *Tylomelania*'s "evolutionary ecology play"

In the central mountain region of the Indonesian island Sulawesi there are two major ancient lake systems, the Malili lakes (Danau Matano, Mahalona, Towuti, Lontoa, and Masapi) and to the northwest, isolated from the former, solitary Lake Poso. These lakes harbour a diverse array of endemic species flocks, comprising Cerithioidea gastropods and bivalves (Corbiculidae), atyid shrimps (*Caridina* H. Milne Edwards, 1837), crabs (Parathelphusidae, Sundatelphusidae) and fishes (Telmatherinidae in the Malili lakes, Atherinidae in Lake Poso) (see Glaubrecht 2010a). In contrast to lakes in the Malili system, the invertebrate fauna of Lake Poso is more disparate and diverse, containing an endemic, cementing corbiculid (erroneously named a distinct genus *Posostrea* Bogan and Bouchet, 1998, see details in Rintelen and Glaubrecht 2006) and an endemic, unusual lymnaeid snail (*Miratesta* Sarasin and Sarasin, 1898, see Albrecht and Glaubrecht 2006, Albrecht *et al.* 2010).

While it was long assumed that this gastropod species flock arose by adaptive radiation (Wesenberg-Lund 1939, Brooks 1950, Davis 1982), the exact nature of this mechanism remained elusive due to lack of data. The few existing species descriptions were typological, sampling density rather low, and data on biology lacking altogether. Following century long neglect, the endemic evolution of the pachychilid gastropods *Tylomelania* Sarasin and Sarasin, 1897 on Sulawesi now offers a most instructive model case for speciation mechanisms and truly adaptive radiations (Table 2), as documented and discussed at length in Rintelen *et al.* (2004, 2007, 2010), Rintelen and Glaubrecht (2005) and Glaubrecht and Rintelen (2008a). A systematic revision of species, including morphology and a molecular phylogeny of *Tylomelania*, provided the prerequisite of a more thorough speciation study testing allopatry, ecology (*e.g.*, habitat preference) and specialization (radular morphology). In addition, the systematic position and biology of the Sulawesi pachychilids have been clarified in relation to other confamiliar Southeast Asian taxa (*e.g.*, Glaubrecht and Rintelen 2003, Köhler *et al.* 2004, Rintelen and Glaubrecht 2005, Köhler and Dames 2009, Köhler and Glaubrecht 2010).

Common ancestry

All 76 pachychilids (44 species plus *ca.* 32 yet undescribed) endemic to Sulawesi have been shown to belong to the viviparous *Tylomelania*, with currently 23 fluviatile (9 plus *ca.* 14 undescribed) and 53 lacustrine species, of which 25 species are in the Lake Poso drainage (with only 7 formally named to date) and 28 species are formally described from the Malili lakes. Monophyly of this clade has been proven in several phylogenetic analyses cited above. Glaubrecht and Rintelen (2003) have shown that the only other pachychilid, *Pseudopotamius* Martens, 1894, disjunctly occurring in the Austral region with two apparently relictual species on the Torres Strait Islands between New Guinea and Australia, is the adelphotaxon of the *Tylomelania* radiation on Sulawesi. Our historical, biogeographic scenario discussed in the former paper suggested an at least Miocene age and vicariant event at the origin of these two lineages. From a molecular clock approach in Köhler and Glaubrecht (2010), it can be concluded that the age of the *Pseudopotamius* and *Tylomelania* lineage is about 30 to 35 my, with the two taxa having separated at about 15 to 20 my ago. However, the actual radiation in rivers and lakes on Sulawesi might be (much) younger (Table 2).

Rapid speciation

Again, the molecular data provide a successful test of both phylogenetic criteria *sensu* Schluter (2000a). Evidence from mitochondrial DNA analyses (COI and 16S, with a total of

1535 bp) with strong support for four clades, suggests four independent colonization events in the Sulawesi lakes, three of these in the Malili lakes plus one in Lake Poso, with riverine taxa being identified as sister groups to three lacustrine clades (Rintelen *et al.* 2004, 2010). The radiations differ considerably in the extent of their diversification, with species numbers and morphotypes, respectively, ranging from three to 25 (Malili 1 clade: 13 spp.; Malili 2: 12 spp.; Malili 3: 3 spp.; and Poso: 25 spp.). Rapid cladogenesis can be inferred from short branch lengths between many basal nodes within each of the four clades (Fig. 3). A separate invasion of Poso and Malili is to be expected, given that these lake systems were never connected. However, it is surprising that colonization took place independently in different ancestral lineages in the three major lakes of the Malili system, which are directly connected by rivers. The high level of support for the four major lake clades contrasts with virtually no resolution at the species level for *Tylomelania*. All lacustrine morphospecies for which more than one specimen or population has been sequenced appear polyphyletic in the molecular phylogeny (Rintelen *et al.* 2004, 2007, Glaubrecht and Rintelen 2008a). This lack of resolution is even more remarkable since there is no lack of genetic structure *per se* in the data, *i.e.*, there are several well supported subclades within three of the four major lake clades. While this pattern may be caused by several factors (see discussion in the general section), a pivotal role for introgressive hybridization is indicated by genotype-phenotype mismatches and preliminary nuclear amplified fragment length polymorphism (AFLP) data (Glaubrecht and Rintelen 2008a, Rintelen *et al.* 2010).

Ecology

Nevertheless, as each colonization event was followed by diversification into an array of morphologically distinct and ecologically specialized species, they provide evidence for the fulfilment of the two remaining ecological criteria for an adaptive radiation *sensu* Schluter (2000a), see Table 2. We found that radular morphology is highly diverse in all lacustrine lineages of *Tylomelania*, with three to six phenotypes found in each clade (Rintelen *et al.* 2004, 2010, Glaubrecht and Rintelen 2008a). In contrast, radular morphology is highly conservative in riverine species. As radular differences having been demonstrated to be indicative of food and substrate preferences (*e.g.*, Hawkins *et al.* 1989), trophic morphology and substrate were found to be highly correlated in all clades. We propose that this allowed several species to coexist sympatrically and syntopically.

All species in the major lakes of the Malili system and Lake Poso are specialized on either soft substrates (mud, sand) or hard substrates (rock, sunken wood), with about 50% of species occurring on either substrate category (Rintelen *et al.* 2007). Some species are specialized on an even

finer scale, *e.g.*, restricted to wood only. Hard substrate taxa in particular show a wide range of mostly substrate- and species-specific radular forms, and there is generally a tight correlation between enlargement of radula denticles and hard substrate. For detailed description and examples see Glaubrecht and Rintelen (2008a) and Rintelen *et al.* (2010), based on data presented in Rintelen *et al.* (2004, 2007). The parallel, substrate-specific occurrence of most radula forms in both ancient lake systems on Sulawesi supports a tight link between radular morphology and substrate. These observations suggest a functional role for differences in trophic morphology, although a detailed understanding of the underlying mechanisms requires further investigation. In concert with the radular differentiation, habitat specialization (substrate and to a lesser degree depth preferences) enables that more than five, possibly up to seven, species of *Tylomelania* coexist at localities with sufficiently structured habitats. This finding becomes even more striking when contrasted with the situation in rivers in general (see below) and with riverine *Tylomelania* on Sulawesi in particular, where only one single species is regularly found, with the exception of sympatric occurrence of three species in the Balocci Valley in Southwest Sulawesi (Table 2). Again, our data suggest a strong role for ecological factors in the diversification and possibly even speciation of *Tylomelania*. We anticipate that parallel situations in several of the lake species provide ideal models to further test for ecological speciation.

However, two factors need to be taken into consideration. First, our detailed studies on selected species and species complexes reveal a more complex and complicated situation. Second, it should not be overlooked that in many cases the species distribution in lacustrine *Tylomelania* is clearly allopatric, *i.e.*, species are essentially confined to one of the three major lakes within the Malili system, where they occur syntopically with other clearly distinct species. This pattern of allopatric occurrence—and presumably speciation—is strong evidence for involvement of geography in speciation within lakes. In addition, we found indications in adult shell and radula characters, and molecular genetics for the possible action of introgressive hybridization in *Tylomelania sarasinorum* Kruimel, 1913 and *T. bakara* Rintelen and Glaubrecht, 2003 in Lake Towuti, as well as many (if not all) species in Lake Mahalona, between the Matano and Towuti lakes (Glaubrecht and Rintelen 2008a). More strikingly, specimens of one fluviatile species are found terminally in one lacustrine clade basically restricted to Lake Towuti, thus similar to the telmatherinid fishes (see Glaubrecht 2010). However, whether hybridization is involved during the speciation process in *Tylomelania* in general has to await more comprehensive data from our ongoing AFLP study (Rintelen and Glaubrecht, unpubl. data).



Figure 3. Molecular phylogeny of the pachychilid gastropod *Tylomelania*, endemic to the Indonesian island of Sulawesi, based on Bayesian inference analysis using mtDNA sequences (COI and 16S, with a total of 1535 bp). A, Phylogram with Malili (M) and P (Poso) lakes taxa, marking four lacustrine clades and independent colonization events. The others are riverine species, with asteriks indicating riverine taxa in terminal position within lacustrine clades. Modified from Rintelen *et al.* (2004). B, C, Detailed sections of BI phylogram based on 660 bp of the COI phylogram for the Poso clade (B) and the Malili 2 clade (C). Reproduced from Rintelen *et al.* (2010).

Contrasting lacustrine species flocks: riverine radiations in Cerithioidean gastropods

Riverine radiations have not attracted the same attention as speciation in lacustrine settings. Rivers around the world hold species-rich assemblages of molluscs, for example, among Cerithioidea, the endemic Pleuroceridae in Tennessee and the Coosa-Cahaba Rivers in the southeastern USA, or the Pachychilidae in Central America (Table 1). Unfortunately, details of their phylogeny, phylogeography and evolution are largely unknown. The few cases among gastropods have been recently reviewed in Glaubrecht and Köhler (2006), and the reader is referred to the literature therein. Only rarely is there convincing evidence for adaptive radiation to have taken place *in situ* in lotic habitats. Nevertheless, riverine cases can shed additional light on the intrinsic and extrinsic properties involved in radiations and the origin of diversification in general, helping to elucidate the evolution of intra-lacustrine species flocks.

As is evident from comparison, for example, both the Congo River drainage and Lake Tanganyika provide stable evolutionary systems, both in their own right and with distinct inherent environmental dimensions. Emphasis has shifted recently to non-lacustrine settings, with studies focussing on various Cerithioidean gastropods in rivers, as reviewed below (see also Table 2). Intralacustrine radiations should not to be seen as evolutionary dead ends, rather, it is possible the repeated switches of limnic taxa between riverine and lacustrine habitats during their evolution guaranteed their survival, and provided ample opportunities for speciation and radiation under various conditions.

Congo River system: *Potadomoides* as Tanganyikan “ancestor”?

The riverine genus *Potadomoides* from the Congo River drainage has proven to be crucial for our understanding of the lacustrine Tanganyikan radiation. Following Brooks (1950: 150) speculation that the thalassoid snails are presumably derived from fluviatile ancestors present at the lake's genesis, Brown (1994: 530) proposed that *Potadomoides* has the strongest claim for consideration in relation to this ancestry (see above).

Common ancestry

Cladistic analyses of morphological data verified the long proposed sister group relationship of lacustrine species of *Lavigeria* (plus *Vinundu*) endemic to Lake Tanganyika and the fluviatile *Potadomoides* from the Congo drainage system, subsumed now under Nassopsinae Kesteven, 1903 (= *Lavigeriinae* Thiele, 1925) (Glaubrecht 1996, 2008a, Glaubrecht and Strong 2007). This fluvio-lacustrine clade, uniting two lacustrine taxa and the fluviatile *Potadomoides*, apparently represents an early independent lineage of East African paludomids

that until recent times survived in and adjacent to Lake Tanganyika. Consequently, while *Potadomoides* certainly does not serve as a suitable model for the majority of the thalassoid gastropods, it might serve as a model for an African paludomid with the potential to colonize not only riverine but also lacustrine habitats.

Rapid speciation and ecology

The species composition was long unresolved, with six species originally described to *Cleopatra* and later transferred to Leloup's new genus (Glaubrecht and Strong 2007). For the recent re-transfer of *C. broeckii*, see Glaubrecht (2010c). In contrast to the type species *P. pelseeneri* Leloup, 1953 which is endemic to the Malagarasi delta, the three other congeneric species are restricted to the upper reaches of the Congo River in eastern Zaire. While it is apparent from the shell morphology of these remaining four taxa as well as their anatomy (in particular reproductive systems) that *Potadomoides* might possess the potential for a profuse radiation in Lake Tanganyika, we lack data as to the age and mode of speciation. Since *Potadomoides* is sister to *Lavigeria*, the molecular analysis of thalassoid paludomids hints at a more recent event. The largely conservative radula morphology clearly supports *Potadomoides* as the adelphotaxon of *Lavigeria* plus *Vinundu*. However, due to the lack of ecological observations from their riverine habitats, we are unable to make inferences as to the mode of speciation, or Schluter's (2000a) criteria. Unfortunately, we lack recent collections of this riverine gastropod, and suitable material for molecular genetic studies. No large-scale exploration of limnic habitats in the Congo Basin has been undertaken for several decades. However, equal to great lakes such as Tanganyika and Malawi, the Congo River and its easternmost tributaries have a species assemblage (not only of unique molluscs) that deserves more attention in the future.

Kaek River, Thailand: unraveling a riverine radiation of *Brotia*

Davis (1982) was first to observe that when *Brotia* is found in rivers in SE Asia, there is usually one species, or two at the most. The only exception to this rule is a small radiation in the Kaek River drainage in north central Thailand, part of the Nan-Chao Phraya system. An exceptional assemblage of morphologically distinct, viviparous species of *Brotia* is endemic to this river system, with seven recognized species exhibiting a remarkable degree of conchological disparity, and with syntopic occurrence of three to four species that are ecologically separated by habitat preferences and trophic specializations (Glaubrecht and Köhler 2006, Köhler *et al.* 2010).

Common ancestry

Based on morphological, molecular phylogenetic data, and phylogeography using mtDNA gene fragments (COI and

16S), it is evident (i) that all species from the Kaek River and adjacent drainages form a monophyletic group of *Brotia* within a large Thai clade, and (ii) that the origin of this Kaek River clade derives from a Mekong River ancestor. In light of the palaeo-hydrological situation of Pleistocene stream capture in accordance with alignments of post-Himalayan river systems, we proposed that together with other faunas pachychilid snails could have been captured and added to the fauna of rivers from the Mekong via the Loei to the Kaek and thus Chao Praya. This would explain the origin of the Kaek River flock in a taxon from the Mekong drainage. Likewise, it is possible that during the complex geological history, with its wide spectrum of tectonic changes affecting the major drainage systems, rivers or at least some of their sections, could have stranded as new lakes, isolating faunas for a million of years or more, and offering ample opportunity for lacustrine radiations. For a more indepth discussion of this and the evolutionary aspects see Glaubrecht and Köhler (2006), and Köhler *et al.* (2010).

Rapid speciation

The relatively shallow topology of the Kaek River gastropods, and the lack of significant resolution in our molecular phylogenies, *i.e.*, the mismatch of gene and species trees, imply a relatively recent origin of this intra-riverine radiation and, consequently, rapid speciation with a high degree of morphological divergence. Thus, again rapid cladogenesis is inferred from short branch lengths within the clades. Several other cases are known where morphologically distinct (sympatric) species have evolved without marked changes in the mitochondrial genome. There are alternative explanations employed in view of lacking greater resolution and flat topology such as incomplete lineage sorting, hybridization which can only be falsified by additional molecular genetic data (see above). Nevertheless, we interpret these data as fulfilment of Schuller's two phylogenetic criteria in the case of the seven *Brotia* species from the Kaek River (Table 2).

Ecology

More difficult to verify is whether there is any phenotype-environment correlation in these unusual *Brotia* species. Along the Kaek River, the syntopic occurrence of up to three or more species was documented during field work. Available data from our first study (Glaubrecht and Köhler 2006) hinted at a similar phenotype-environment correlation as in lacustrine *Tylomelania*. In several locations along the Kaek River, preliminary work indicated that habitat preferences of individual *Brotia* species correlate with their radula morphology. Again, trait utility could not be tested (Table 2). However, Köhler *et al.* (2010) are more cautious as to the ecological adaptation criterion, suggesting that there is no such correlation and/or trophic specialization. More sophis-

ticated studies are necessary to establish the eminent role of spatial factors in evolution, highlighting the importance of local, adaptive divergence for geographical patterns of speciation. Representing a riverine radiation of a monophyletic species flock with presumably relatively recent diversification, two questions still remain unresolved: (i) the origin of the Kaek River species of *Brotia* from a colonist derived from the Mekong drainage and subsequent river capture providing a possible hydrological explanation, and (ii) the causation for an *in situ* speciation along the river and the contribution of geographical (*i.e.*, historical) versus ecological factors.

Madagascar: rediscovering a radiation in *Madagasikara*

Recently, an overlooked riverine radiation of Cerithioid-eans has been uncovered on Madagascar. Renowned for its rich and diverse biota that evolved during lengthy isolation, the continental island also harbours pachychilid taxa that were traditionally attributed to *Melanatria* Bowdich, 1822. This name, however, is an objective synonym, thus not available and replaced now by the new genus name *Madagasikara* Köhler and Glaubrecht, 2010. A considerable number of formal species-group names have historically been affiliated with this group, suggesting a considerable degree of morphological diversity mainly in the shell, as this was the feature traditionally emphasized by conchologists. While recent authors stated that this diversity only mirrors infraspecific variability of one or two valid species, other studies of pachychilid gastropods revealed that overemphasis on intra-specific variability in freshwater snails might result in a significant underestimation of species diversity. Taxonomic revisions using modern evolutionary systematic approaches are needed to assess species limits and provide the framework for the study of speciation and radiation.

Common ancestry

By analyzing morphology and molecular genetics (based on a mtDNA fragment of the 16S gene), we found that the diversity of this group has been underestimated, resulting in the description of three new species in addition to the two species previously recognised. Using a mitochondrial phylogeny that includes all currently accepted pachychilid genera and a strict molecular clock approach with two alternative calibrations, we found that the origin of the family Pachychilidae was no more than 50 mya, whereas the origin of the Madagascar lineage is estimated as between 15–31 mya, approximately concurrent with the colonization events in a number of other Madagascar animal taxa.

Rapid speciation

With the differentiation of the five named Madagascan species starting probably not before 10 mya, the pachychilid

radiation on the island appears to be not older than 3 to 5 mya. The topology of this section of the molecular phylogeny hints at a rapid radiation event that led to the colonization of all major river systems of the island (with the exception of the drier southwest). As the *Madagasikara* species of our phylogeny have non-overlapping occurrences, in contrast to the exceptional riverine radiation reported for Kaek River pachychilids, we conclude allopatric speciation in their case. However, given the paucity of material and imprecise localities for older museum collections, an explanation of the evolutionary history of *Madagasikara* and regional patterns of speciation is premature. The diversity and fragmentation of freshwater habitats on this island is associated with considerable levels of local endemism, and in many freshwater groups the majority of species are restricted to single rivers or creeks.

Ecology

We found five species of *Madagasikara* to inhabit Madagascar, with just one species occurring in any one river or river system. While the east coast with its short rivers is inhabited by two species, the remaining species occur in restricted regions along the north and northwest of the island. Thus, not only is there an unrecognised radiation in *Madagasikara* with species-level differentiation in particular along the drainages of the northwest of the island, but our analyses also suggest a spatial bi-partitioning along the mountainous N-S axis of Madagascar. A comparison of shell features reveals that species with shells dominated by spiral elements (and axial elements completely lacking) are restricted to the west and north of the island. In contrast, along the east coast, the two species exhibit pronounced axial elements in combination with a strongly stepped shape of the shell. Hardly any other information is available from the field to put this conchological differentiation into perspective. In addition, conservative radula morphology does not hint at trophic specialization as documented in particular in lacustrine *Tylomelania*. Instead it resembles the pattern found for riverine pachychilids on Sulawesi and in Thailand (with the exception of the case of *Brotia* in Kaek River, see above).

Summary: Speciation from a snails' perspective

From the above review it is evident that not only the two different model lake systems and their respective faunal elements, but also riverine settings are distinct with respect to the influence of intrinsic factors (e.g., crucial biological features such as viviparity, dispersal and trophic specialization) versus extrinsic factors (e.g., palaeohydrology, habitat fragmentation, drainage systems). Although lotic systems are generally considered harsh environments (as determined by physical factors and stochastic events reducing densities), they are more permanent on both ecological and evolutionary

timescales than most lake habitats. The only notable exception are ancient lakes, which provide ample opportunity for many different organisms to speciate, in contrast to rivers where environmental changes are gradual and do not prevent gene flow. Interestingly, rarely have true riverine radiations been recognized, and the only known cases from Cerithioidean gastropods were discussed above.

As is evident from Table 2, in all cases we have evidence not only for common ancestry but also for a fairly recent origin and rapid speciation with rapid morphological divergence, parallel to the recent diversification of pachychilid species flocks in the ancient lakes on Sulawesi and the *Lavigeria* radiation in Lake Tanganyika. Within each of these clades, a burst of very recent radiations resulted in a partial mismatch of species and gene trees. Apparently, rates of molecular and morphological evolution have been highly divergent in lake species (as opposed to widespread riverine taxa). While there is evidence for trophic specialization linked with differential habitat use within the lakes on Sulawesi, indicating ecological speciation in *Tylomelania*, allopatric mechanisms might also have been involved.

In contrast, the Kaek River with its sympatric and partly syntopic species flock reveals conditions where speciation through allopatric isolation seems implausible, quite to the contrary of *Madagasikara* on Madagascar. This strongly hints at spatial segregation, for example, by trophic substrate specialization correlated with adaptation in radula morphology to different microphagous grazing, as the ultimate trigger of speciation in Kaek River species which, however, remains to be shown. On a finer scale, and exemplified by adequate case studies, future comparative work on the Sulawesi lakes with their relatively large species flocks contrasted with the less species-rich Kaek River group in Thailand and species on Madagascar might help in elucidating these aspects of radiation and origin of diversification.

Although large species inventories and high levels of endemism have been reported for other freshwater gastropods from lotic systems, among them, for example, the North American Pleuroceridae, speciation mechanisms (including allopatric versus ecological speciation models) have not been considered, investigated, or often even discussed. Attempts to evaluate these factors suffered from lack of insight into systematics and morphology (i.e., the reproductive biology) of the limnic gastropods involved, and how crucial differences in the geological setting were, such as e.g., rifting in the ca. 12 myr old Lake Tanganyika versus Sulawesi's composite terrane origin with ca. 1-2 myr old lakes.

In summary, we arrive at the following conclusions: (i) Allopatry: The allopatric speciation model offers a well-supported starting point for the explanation of the existence of species flocks in *Tylomelania* at least in the Malili lakes (but not Lake Poso) on Sulawesi. The same is most likely for

riverine cases, such as *Potadomoides* in the Congo River and *Madagasikara* on Madagascar. (ii) Ecology: Substrate preference found in most lacustrine (and riverine) species as well as trophic specialization studied so far in more detail in some *Tylomelania* species hint at the importance and relevance of ecological factors responsible for the coexistence of species. However, we lack clear evidence that competition-driven specialization was the ultimate cause of speciation, or that adaptation and trophic morphology were drivers for the radiation in the case of the *Brotia* species from the Kaek River. (iii) Complexity: Exemplary studies of individual species, in particular those of lacustrine *Tylomelania* and riverine *Brotia* from Kaek River revealed that contingency plays a role and that the evolutionary history of freshwater gastropods in lacustrine as well as riverine settings is more complex than assumed earlier. As we have so far utilized essentially the more easily available mitochondrial genes, other potentially relevant factors and processes that drive speciation and radiation (e.g., ecology, adaptation, natural selection, hybridization) can often only be assumed, and these need to be tested in more detail in the field.

CONCLUSION

"A scientific revolution that makes no difference to everyday scientific work seems an odd sort of revolution." Endersby (2009: 1499)

We came a long way to understand how new species originate, which remained Darwin's "mystery of mysteries". Since speciation is the underlying mechanism for radiation, it is the ultimate causation for the biological diversity of life that surrounds us. While the great importance of speciation and of adaptive (and non-adaptive) radiations for biodiversity is widely accepted, our understanding of the processes and mechanisms involved is still limited. Any broader generalization needs to be based on the accumulation of more evidence from additional case studies, which freshwater gastropods can offer in many different environmental settings. In addition, today there is a variety of current approaches in evolutionary research to study speciation.

The use of modern techniques from molecular biology, bioinformatics and systematic phylogeny allow reconstructing the relationships of organisms, the course of evolution and its underlying causation. Many model cases using these techniques show the progress and dynamics of this kind of research. At the same time it has become clear (i) that the phylogenetic patterns revealed by phylogenetic trees (irrespective of the individual genes and algorithms used) offer only a first approach and proxy for species richness, speciation mode and (adaptive) radiation, (ii) that palaeontological patterns often lack the temporal-spatial resolution

to resolve speciation and detect the responsible mechanism, (iii) that models such as Cerithioidean gastropods in insular, but rarely in other "natural laboratories" provide us with species flocks that allow for detailed and sophisticated studies of these mechanisms.

Finally, I conclude that allopatric speciation should still be used as a null-hypothesis for testing and falsifying non-allopatry by studying ecological and other relevant factors. It remains to be shown whether and to which degree ecological (and sympatric) speciation is involved in the origin of species flocks and whether for example trophic specializations can provide evidence for natural selection playing an ultimate role in the process of speciation and radiation. Although these phenomena may no longer be the same "mystery of mysteries" for us as it once was for Darwin, our answers are not completely satisfactory yet, with many questions still remaining unanswered.

ACKNOWLEDGMENTS

I am indebted to Warren Allmon for inviting me to the speciation symposium in July 2009 at Cornell University during the AMS 75th Anniversary meeting in Ithaca, New York, and to the participants for fruitful discussions. I also thank the American Malacological Society for supporting my travel to Ithaca, and Ken Brown for many helpful comments and linguistic corrections to an earlier version of the manuscript. Without students and colleagues jointly studying limnic gastropods with me over the last decade at the Berlin Museum, this paper would not have been possible, so I thank for their participation and inspiration Frank Köhler, Thomas von Rintelen, Henning Scholz, Ellen Strong and Tony Wilson. Work referred to herein was substantially and continuously supported by several research grants awarded to me from the Deutsche Forschungsgemeinschaft DFG (grants no. GL 297/1-1, 1-2, 297/2-1, 2-2, 297/4-1, 4-2, 297/5-1, 297/7-1, 7-2 and 7-3, 297/15-1, 15-2, 445 KEN-18/02+3/06).

LITERATURE CITED

- Albrecht, C. and M. Glaubrecht. 2006. Brood care among basommatophorans: A unique reproductive strategy in the freshwater limpet snail *Protancylus* (Heterobranchia: Protancylidae), endemic to ancient lakes on Sulawesi, Indonesia. *Acta Zoologica* 87: 49-58.
- Albrecht, C., M. Benke, T. v. Rintelen, and M. Glaubrecht. 2010. Evolution of an enigmatic freshwater limpet – the genus *Protancylus* (Hydrophila: Planorbidae) endemic to ancient lakes on Sulawesi, Indonesia. In: S. Panha, C. Sutcharit, and P. Tongkerd, eds., *Abstracts of the 17th World Congress of Malacology, 18-24 July 2010, Phuket, Thailand*. Tropical Natural History, Supplement 3: 309. Chulalongkorn University Museum of Natural History, Bangkok.

- Allmon, W. D. 1992. A causal analysis of stages in allopatric speciation. *Oxford Surveys in Evolutionary Biology* 8: 219-257.
- Allmon, W. D. and U. E. Smith. 2011. What, if anything, can we learn from the fossil record about speciation in marine gastropods? Biological and geological considerations. *American Malacological Bulletin* 29: 247-276.
- Awise, J. C. 2006. The ontogeny of molecular ecology. *Molecular Ecology* 15: 2687-2689.
- Bandel, K. 2000. Speciation among the Melanopsidae (Caenogastropoda). Special emphasis to the Melanopsidae of the Pannonian Lake at Pontian time (Late Miocene) and the Pleistocene and Recent of Jordan. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 84: 131-208.
- Barluenga, M., K. N. Stölting, W. Salzburger, M. Muschick, and A. Meyer. 2006. Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature* 439: 719-723.
- Barlow, G. W. 2000. *The Cichlid Fishes: Nature's Grand Experiment in Evolution*. Perseus Publishing, Cambridge, Massachusetts.
- Barlow, N., ed., 1963. Darwin's Ornithological Notes. With an introduction, notes, and appendix by Nora Barlow. *Bulletin of the British Museum (Natural History)*, Historical Series 2: 201-278.
- Barracough, T. G. 2004. Theory of speciation: Filling an empty hole. *Trends in Ecology and Evolution* 19: 569-570.
- Barracough, T. G. and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* 155: 419-434.
- Benke, M., M. Brändle, C. Albrecht, and T. Wilke. 2009. Pleistocene phylogeography and phylogenetic concordance in cold-adapted spring snails (*Bythinella* spp.). *Molecular Ecology* 18: 890-903.
- Benton, M. J. and P. N. Pearson. 2001. Speciation in the fossil record. *Trends in Ecology and Evolution* 16: 405-411.
- Bichain, J. M., P. Gaubert, S. Samadi, and M. C. Boisselier-Dubayle. 2007. A gleam in the dark: Phylogenetic species delimitation in the confusing spring-snail genus *Bythinella* Moquin-Tandon, 1856 (Gastropoda: Rissoidea: Amnicolidae). *Molecular Phylogenetics and Evolution* 45: 927-941.
- Bilton, D. T., J. R. Freeland, and B. Okamura. 2001. Dispersal in freshwater invertebrates. *Annual Review in Ecology and Systematics* 32: 159-181.
- Bock, W. J. 2004. Species: The concept, category and taxon. *Journal of Zoological Systematics and Evolutionary Research* 42: 178-190.
- Bohonak, A. J. and D. G. Jenkins. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* 6: 783-796.
- Bolnick, D. I. and B. M. Fitzpatrick. 2007. Sympatric speciation: Models and empirical evidence. *Annual Review in Ecology, Evolution and Systematics* 38: 459-487.
- Boss, K. J. 1978. On the evolution of gastropods in ancient lakes. In: V. Fretter and J. F. Peake, eds, *Pulmonates, 2A: Systematics, Evolution and Ecology*. Academic Press, London. Pp. 385-428.
- Brooks, J. L. 1950. Speciation in ancient lakes. *Quarterly Review of Biology* 25: 131-176.
- Browne, J. 2002. *Charles Darwin. The Power of Place*. Alfred A. Knopf, New York.
- Bush, G. L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* 23: 237-251.
- Bush, G. L. 1975. Modes of animal speciation. *Annual Review of Ecology and Systematics* 6: 339-364.
- Bush, G. L. 1994. Sympatric speciation in animals: New wine in old bottles. *Trends in Ecology and Evolution* 9: 285-288.
- Bush, G. L. and J. J. Smith. 1998. The genetics and ecology of sympatric speciation: A case study. *Research in Population Ecology* 40: 175-187.
- Butlin, R., J. Bridle, and D. Schluter. 2009. *Speciation and Patterns of Diversity*. Ecological Reviews Series. Cambridge University Press, Cambridge, UK.
- Cain, J. 2009. Rethinking the synthesis period in evolutionary studies. *Journal of the History of Biology* 42: 621-648.
- Cain, J. and M. Ruse. 2009. *Descended from Darwin. Insights into the History of Evolutionary studies, 1900-1970*. American Philosophical Society, Philadelphia.
- Carson, H. L. and K. Y. Kaneshiro. 1976. *Drosophila* of Hawaii: Systematics and ecological genetics. *Annual Review of Ecology and Systematics* 7: 311-345.
- Colgan, D. J. and W. F. Ponder. 2000. Incipient speciation in aquatic snails in an arid-zone spring complex. *Biological Journal of the Linnean Society* 71: 625-641.
- Colosimo, P. F., K. E. Hosemann, S. Balabhadra, G. Villarreal, Jr., M. Dickson, J. Grimwood, J. Schmutz, R. M. Myers, D. Schluter, and D. M. Kingsley. 2005. Widespread parallel evolution in sticklebacks by repeated fixation of ectodysplasin alleles. *Science* 307: 1928-1933.
- Collin, R. 2001. The effects of mode of development on phylogeography and population structure of North Atlantic *Crepidula* (Gastropoda: Calyptraeidae). *Molecular Ecology* 10: 2249-2262.
- Collin, R. 2003. Phylogenetic relationships among calyptraeid gastropods and their implications for the biogeography of marine speciation. *Systematic Biology* 52: 618-640.
- Corsi, P. 1988. *The Age of Lamarck. Evolutionary Theories in France 1790-1830*. University of California Press, Berkeley.
- Coulter, G. W., ed., 1991. *Lake Tanganyika and its Life*. Oxford University Press, Oxford.
- Cowie, R. H. 1992. Evolution and extinction of Partulidae, endemic Pacific island land snails. *Philosophical Transactions of the Royal Society London (B)* 335: 167-191.
- Coyne, J. A. and H. A. Orr. 2004. *Speciation*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- Darwin, F., ed., 1909. *The Foundations of the Origin of Species, by Charles Darwin*. Cambridge University Press, Cambridge, UK.
- Davis, G. M. 1982. Historical and ecological factors in the evolution, adaptive radiation, and biogeography of freshwater mollusks. *American Zoologist* 22: 375-395.
- Desmond, A. and J. Moore. 1991. *Darwin. The Life of a Tormented Evolutionist*. Warner Books, New York.
- Dieckmann, U. and M. Doebeli. 1999. On the origin of species by sympatric speciation. *Nature* 400: 354-357.

- Dillon, R. T. and R. C. Frankis. 2004. High levels of mitochondrial DNA sequence divergence in isolated populations of freshwater snails of the genus *Goniobasis*. *American Malacological Bulletin* **19**: 69-77.
- Dillon, R. T. and J. D. Robinson. 2009. The snails the dinosaurs saw: Are the pleurocerid populations of the Older Appalachians a relict of the Paleozoic Era? *Journal of North American Benthological Society* **28**: 1-11.
- Dobzhansky, T. 1951. *Genetics and the Origin of Species*. Columbia University Press, New York.
- Doebeli, M. 1996. A quantitative genetic competition model for sympatric speciation. *Journal of Evolutionary Biology* **9**: 893-909.
- Doebeli, M. and U. Dieckmann. 2003. Speciation along environmental gradients. *Nature* **421**: 259-264.
- Duda, T. F., M. B. Bolin, C. P. Meyer, and A. J. Kohn. 2008. Hidden diversity in a hyperdiverse gastropod genus: Discovery of previously unidentified members of a *Conus* species complex. *Molecular Phylogenetics and Evolution* **49**: 867-876.
- Ebachs, M. C. and M. de Carvalho. 2010. Anti-intellectualism in the DNA barcoding enterprise. *Zoologia* **27**: 165-178.
- Eldredge, N. and S. J. Gould 1972. Punctuated equilibria: An alternative to phyletic gradualism. In: T. J. M. Topf, ed., *Models in Paleobiology*. Freeman, Cooper and Co., San Francisco. Pp. 82-115.
- Emerson, B. C. 2008. Speciation on islands: What are we learning? *Biological Journal of the Linnean Society* **95**: 47-52.
- Endersby, J. 2009. Lumpers and splitters: Darwin, Hooker, and the search for order. *Science* **326**: 1496-1499.
- Endler, J. A. 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton.
- Feder, J. L., C. A. Chilcote, and G. L. Bush. 1988. Genetic differentiation between sympatric host races of the apple maggot fly *Rhagoletis pomonella*. *Nature* **336**: 61-64.
- Fehér, Z., M. L. Zettler, M. Bozsó, and K. Szabó. 2009. An attempt to reveal the systematic relationship between *Theodoxus prevostianus* (C. Pfeiffer, 1828) and *Theodoxus danubialis* (C. Pfeiffer, 1828) (Mollusca, Gastropoda, Neritidae). *Mollusca* **27**: 95-107.
- Foster, S. A. and J. A. Baker. 2004. Evolution in parallel: New insights form a classic system. *Trends in Ecology and Evolution* **19**: 456-459.
- Fryer, G. 1991. Comparative aspects of adaptive radiation and speciation in Lake Baikal and the great rift lakes of Africa. *Hydrobiologia* **211**: 137-146.
- Fryer, G. 1996. Endemism, speciation and adaptive radiation in great lakes. *Environmental Biology of Fishes* **45**: 109-131.
- Fryer, G. and T. D. Iles. 1972. *The Cichlid Fishes of the Great Lakes of Africa*. Oliver and Boyd, Edinburgh.
- Funk, D. J. and K. E. Omland. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology and Systematics* **34**: 397-423.
- Gavrilets, S. 2004. *Fitness Landscapes and the Origin of Species*. Monographs in Population Biology 41. Princeton University Press, Princeton.
- Gavrilets, S. and J. B. Losos. 2009. Adaptive radiation: Contrasting theory with data. *Science* **323**: 732-737.
- Gavrilets, S., H. Li, and M. D. Vose. 2000. Patterns of parapatric speciation. *Evolution* **54**: 1126-1134.
- Gittenberger, E. 1988. Sympatric speciation in snails: A largely neglected model. *Evolution* **42**: 826-828.
- Glaubrecht, M. 1993. Mapping the diversity: Geographical distribution of the freshwater snail *Melanopsis* (Gastropoda: Cerithioidea: Melanopsidae) with focus on its systematics in the Mediterranean Basin. - *Mitteilungen aus dem Hamburger Zoologisches Museum und Institut* **90**: 41-97.
- Glaubrecht, M. 1996. *Evolutionsökologie und Systematik am Beispiel von Süß- und Brackwasserschnecken (Mollusca: Caenogastropoda: Cerithioidea): Ontogenese-Strategien, paläontologische Befunde und Historische Zoogeographie*. Backhuys Publishers, Leiden [In German with extended English abstract].
- Glaubrecht, M. 1999. Systematics and the evolution of viviparity in tropical freshwater gastropods (Cerithioidea: Thiaridae sensu lato) – an overview. *Courier Forschungs-Institut Senckenberg* **215**: 91-96.
- Glaubrecht, M. 2000. A look back in time: Toward an historical biogeography as synthesis of systematic and geologic patterns outlined with limnic gastropods. *Zoology: Analysis of Complex Systems* **102**: 127-147.
- Glaubrecht, M. 2002. The “experience” of nature: From Salomon Müller to Ernst Mayr, or The insights of travelling naturalists toward a zoological geography and evolutionary biology. *Verhandlungen zur Geschichte und Theorie der Biologie* **9**: 245-282.
- Glaubrecht, M. 2004. Leopold von Buch's legacy: Treating species as dynamic natural entities, or why geography matters. *American Malacological Bulletin* **19**: 111-134.
- Glaubrecht, M. 2006. Independent evolution of reproductive modes in viviparous freshwater Cerithioidea (Gastropoda, Sorbeoconcha) – a brief review. *Basteria* **69** (Supplement 3): 28-32.
- Glaubrecht, M. 2007a. Die Ordnung des Lebendigen. Zur Geschichte und Zukunft der Systematik in Deutschland. In: J. W. Wägele, ed., *Höhepunkte der zoologischen Forschung im deutschen Sprachraum. Festschrift zur 100. Jahresversammlung der Deutschen Zoologischen Gesellschaft in Köln*. Basiliken Press, Marburg. Pp. 59-110 [In German].
- Glaubrecht, M. 2007b. “Biological” species and their discovery: The tradition of species research at the Berlin Natural History Museum. In: M. Glaubrecht, A. Kinitz, and U. Moldzyk, eds., *Evolution in Action*. Prestel, München. Pp. 44-55.
- Glaubrecht, M. 2008a. Adaptive radiation of thalassoid gastropods in Lake Tanganyika, East Africa: Morphology and systematization of a paludomid species flock in an ancient lake. *Zoosystematics and Evolution* **84**: 71-122.
- Glaubrecht, M. 2008b. Hard facts about soft animals. *Science* **320**: 1014-1015.
- Glaubrecht, M. 2009. On “Darwinian Mysteries” or molluscs as models in evolutionary biology: From local speciation to global radiation. *American Malacological Bulletin* **27**: 2-23.
- Glaubrecht, M., ed. 2010a. *Evolution in Action. Case studies in Adaptive Radiation, Speciation and the Origin of Biodiversity*. Springer, Heidelberg.

- Glaubrecht, M. 2010b. Introduction to the Symposium on Speciation: Insights from Insular Environments to Global Patterns. In: S. Panha, C. Sutcharit, and P. Tongkerd, eds., *Abstracts of the 17th World Congress of Malacology, 18-24 July 2010, Phuket, Thailand*. Tropical Natural History, Supplement 3. P. 163. Chulalongkorn University Museum of Natural History, Bangkok.
- Glaubrecht, M. 2010c. The enigmatic *Cleopatra broeckii* Putzeys, 1899 of the Congo River system in Africa – re-transfer from *Potadomoides* Leloup, 1953 (Caenogastropoda, Cerithioidea, Paludomidae). *Zoosystematics and Evolution* **86**: 283-293.
- Glaubrecht, M. and T. v. Rintelen. 2003. Systematics, molecular genetics and historical zoogeography of the viviparous freshwater gastropod *Pseudopotamis* (Cerithioidea, Pachychilidae): A relic on the Torres Strait Islands, Australia. *Zoologica Scripta* **32**: 415-435.
- Glaubrecht, M. and F. Köhler. 2004. Radiating in a river: Systematics, molecular genetics and morphological differentiation of viviparous freshwater gastropods endemic to the Kaek River, central Thailand (Cerithioidea, Pachychilidae). *Biological Journal of the Linnean Society* **82**: 275-311.
- Glaubrecht, M. and E. E. Strong. 2007. Ancestry to an endemic radiation in Lake Tanganyika? Evolution of the viviparous gastropod *Potadomoides* Leloup, 1953 in the Congo River system (Cerithioidea, Paludomidae). *Biological Journal of the Linnean Society* **92**: 367-401.
- Glaubrecht, M. and T. v. Rintelen. 2008a. The species flocks of lacustrine gastropods: *Tylomelania* on Sulawesi as models in speciation and adaptive radiation. Proceedings of the "Speciation in Ancient Lake IV" Symposium, Berlin. *Hydrobiologia* **615**: 181-199.
- Glaubrecht, M. and T. v. Rintelen. 2008b. The first comprehensive molecular phylogeny reveals ancient vicariance, parallel evolution of viviparity and extensive convergence in shell morphology of thiarid freshwater gastropods. In: R. Willmann, ed., *Abstracts 10. Jahrestagung der Gesellschaft für Biologische Systematik*. Universitätsverlag, Göttingen.
- Glaubrecht, M. and T. v. Rintelen. 2009. From Poe to Ponder...and Lindberg: Introduction to the symposium "Molluscs as models in evolutionary biology". *American Malacological Bulletin* **27**: 1-2.
- Glaubrecht, M. and J. Haffer. 2010. Classifying nature: Constantin W. L. Gloger's (1803-1863) tapestry of a "Natural System of the Animal Kingdom". *Zoosystematics and Evolution* **86**: 81-115.
- Glaubrecht, M., H. Scholz, and J. C. A. Joordens. 2009. Molluscs of the ancient palaeo-lake Lorenyang, Turkana Basin: Anagenesis vs. cladogenesis and the migration of faunas. *Abstract 6th Meeting Speciation in Ancient Lakes, Ohrid, Macedonia, September 2009*: wp.
- Glor, R. E. 2010. Phylogenetic insights on adaptive radiation. *Annual Review in Ecology, Evolution and Systematics* **41**: 251-270.
- Görthner, A. 1992. Bau, Funktion und Evolution komplexer Gastropodenschalen in Langzeit-Seen. Mit einem Beitrag zur Paläobiologie von *Gyraulus "multiformis"* im Steinheimer Becken. *Stuttgarter Beiträge zur Naturkunde* **190B**: 1-173 [In German].
- Gould, S. J. and N. Eldredge. 1993. Punctuated equilibrium comes of age. *Nature* **366**: 223-227.
- Gourbiere, S. 2004. How do natural and sexual selection contribute to sympatric speciation? *Journal of Evolutionary Biology* **17**: 1297-1309.
- Grant, P. R. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton.
- Grant, P. R. 2001. Geographical speciation. *Evolution* **59**: 1880-1882.
- Grant, P. R. and B. R. Grant. 2008. *How and Why Species Multiply. The Radiation of Darwin's Finches*. Princeton University Press, Princeton.
- Grant, P. R. and B. R. Grant. 2009. The secondary contact phase of allopatric speciation in Darwin's finches. *Proceedings of the National Academy of Science* **106**: 20141-20148.
- Haase, M., T. Wilke, and P. Mildner. 2007. Identifying species of *Bythinella* (Caenogastropoda: Rissoidea): A plea for an integrative approach. *Zootaxa* **1563**: 1-16.
- Harvey, M. S. 2002. Short-range endemism among the Australian fauna: Some examples from non-marine environments. *Invertebrate Systematics* **16**: 555-570.
- Hawkins, S. J., D. C. Watson, A. S. Hill, S. P. Harding, M. A. Kyriakides, S. Hutchinson, and T. A. Norton. 1989. A comparison of feeding mechanisms in microphagous, herbivorous, intertidal, prosobranchs in relation to resource partitioning. *Journal of Molluscan Studies* **55**: 151-165.
- Hawthorne, D. J. and S. Via. 2001. Genetic linkage of ecological specialization and reproductive isolation in pea aphids. *Nature* **412**: 904-907.
- Hayes, K. A., R. H. Cowie, and S. C. Thiengo. 2009a. A global phylogeny of apple snails: Gondwana origin, generic relationships, and the influence of outgroup choice (Caenogastropoda: Ampullariidae). *Biological Journal of the Linnean Society* **98**: 61-76.
- Hayes, K. A., R. H. Cowie, A. Joergensen, R. Schultheiß, C. Albrecht, and S. C. Thiengo. 2009b. Molluscan models in evolutionary biology: Apple snails (Caenogastropoda: Ampullariidae) as a system for addressing fundamental questions. *American Malacological Bulletin* **27**: 47-58.
- Heads, M. 2009. Inferring biogeographic history from molecular phylogenies. *Biological Journal of the Linnean Society* **98**: 757-774.
- Hellberg, M. E. 1998. Sympatric sea shells along the sea's shore: The geography of speciation in the marine gastropod *Tegula*. *Evolution* **52**: 1311-1324.
- Hendry, A. P., P. Nosil, and L. Rieseberg. 2007. The speed of ecological speciation. *Functional Ecology* **21**: 455-464.
- Hendry, A. R. 2008. Darwin in the fossils. *Nature* **451**: 779-780.
- Hendry, A. R. 2009. Speciation. *Nature* **458**: 162-163.
- Hershler, R. and H.-P. Liu. 2008. Ancient vicariance and recent dispersal of springsnails (Hydrobiidae: Pyrgulopsis) in the Death Valley system, California-Nevada. In: M. C. Reheis, R. Hershler, and D. M. Miller, eds., *Late Cenozoic Drainage History of the Southwestern Great Basin and Lower Colorado River Region. Geological and Biotic Perspectives*. Geological Society of America *Special Papers* **439**: 91-101.
- Hershler, R., M. Mulvey, and H.-P. Liu. 2005. Genetic variation in the desert springsnail (*Tryonia porrecta*): Implications for reproductive mode and dispersal. *Molecular Ecology* **14**: 1755-1765.

- Heuer, P. 2008. *Art, Gattung, System. Eine logisch-systematische Analyse biologischer Grundbegriffe*. Verlag Karl Alber, Freiburg, München [In German].
- Hey, J., R. S. Waples, M. L. Arnold, R. K. Butlin, and R. G. Harrison. 2003. Understanding and confronting species uncertainty in biology and conservation. *Trends in Ecology and Evolution* **18**: 597-603.
- Hickerson, M. J., B. C. Carstens, J. Cavender-Bares, K. A. Crandall, C. H. Graham, J. B. Johnson, L. Rissler, P. F. Victoriano, and A. D. Yoder. 2010. Phylogeography's past, present, and future: 10 years after Avise, 2000. *Molecular Phylogenetics and Evolution* **54**: 291-301.
- Holznagel, W. E. and C. Lydeard. 2000. A molecular phylogeny of North American Pleuroceridae (Gastropoda: Cerithioidea) based on mitochondrial 16S rDNA sequences. *Journal of Molluscan Studies* **66**: 233-257.
- Hoskin, C. J., M. Higgie, K. R. McDonald, and C. Moritz. 2005. Reinforcement drives rapid allopatric speciation. *Nature* **437**: 1353-1356.
- Hull, D. K. 1989. *The Metaphysics of Evolution*. State University of New York Press, Albany.
- Hutchinson, G. H. 1965. *The Ecological Theater and the Evolutionary Play*. Yale University Press, New Haven.
- Irschick, D., L. Dyer, and T. W. Sherry. 2005. Phylogenetic methodologies for studying specialization. *Oikos* **110**: 404-408.
- Irwin, D. E., S. Bensch, and T. D. Price. 2001. Speciation in a ring. *Nature* **409**: 333-337.
- Irwin, D. E., S. Bensch, J. H. Irwin, and T. D. Price. 2005. Speciation by distance in a ring species. *Science* **307**: 414-416.
- Jiggins, C. D. and J. R. Bridle. 2004. Speciation in the apple maggot fly: A blend of vintages? *Trends in Ecology and Evolution* **19**: 111-114.
- Johannesson, K. 2001. Parallel speciation: A key to sympatric divergence. *Trends in Ecology and Evolution* **16**: 148-153.
- Johannesson, K. 2009. Inverting the null-hypothesis of speciation: A marine snail perspective. *Evolutionary Ecology* **23**: 5-16.
- Johannesson, K., E. Rolán-Alvarez, and A. Ekendahl. 1995. Incipient reproductive isolation between two sympatric morphs of the intertidal snail *Littorina saxatilis*. *Evolution* **49**: 1180-1190.
- Johannesson, K. and C. André. 2006. Life on the margin: Genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. *Molecular Ecology* **15**: 2013-2029.
- Johnson, M. S., J. Murray, and B. Clarke. 1993. The ecological genetics and adaptive radiation of *Partula* on Moorea. *Oxford Surveys in Evolutionary Biology* **9**: 167-238.
- Jordaens, K., P. van Riel, A. M. Frias Martins, and T. Backeljau. 2009. Speciation on the Azores islands: Congruent patterns in shell morphology, genital anatomy, and molecular markers in endemic land snails (Gastropoda, Leptaxinae). *Biological Journal of the Linnean Society* **97**: 166-176.
- Junker, T. and U. Hoßfeld. 2002. The architects of the evolutionary synthesis in national socialist Germany: Science and politics. *Biology and Philosophy* **17**: 223-249.
- Köhler, F. and C. Dames. 2009. Phylogeny and systematics of the Pachychilidae of mainland South-East Asia – novel insights from morphology and mitochondrial DNA (Mollusca, Caenogastropoda, Cerithioidea). *Zoological Journal of the Linnean Society* **157**: 697-699.
- Köhler, F. and G. Deen. 2010. Hybridisation as potential source of incongruence in the morphological and mitochondrial diversity of a Thai freshwater gastropod (Pachychilidae, *Brotia* H. Adams, 1866). *Zoosystematics and Evolution* **86**: 301-314.
- Köhler, F. and M. Glaubrecht. 2001. Toward a systematic revision of the Southeast Asian freshwater gastropod *Brotia* H. Adams, 1866 (Cerithioidea: Pachychilidae): An account of species from around the South China Sea. *Journal of Molluscan Studies* **67**: 281-318.
- Köhler, F. and M. Glaubrecht. 2003. Morphology, reproductive biology and molecular genetics of ovoviviparous freshwater gastropods (Cerithioidea, Pachychilidae) from the Philippines, with description of a new genus *Jagora*. *Zoologica Scripta* **32**: 35-59.
- Köhler, F. and M. Glaubrecht. 2006. A systematic revision of the Southeast Asian freshwater gastropod *Brotia* (Cerithioidea: Pachychilidae). *Malacologia* **48**: 159-251.
- Köhler, F. and M. Glaubrecht. 2007. Out of Asia and into India: On the molecular phylogeny and biogeography of the endemic freshwater pachychilid gastropod *Paracrostoma* Cossmann, 1900 (Caenogastropoda: Pachychilidae). *Biological Journal of the Linnean Society* **91**: 627-651.
- Köhler, F. and M. Glaubrecht. 2010. Uncovering an overlooked radiation: Morphological and mitochondrial DNA differentiation in endemic freshwater snails on Madagascar (Caenogastropoda: Pachychilidae) and their biogeography. *Biological Journal of the Linnean Society* **99**: 867-894.
- Köhler, F., T. V. Rintelen, A. Meyer, and M. Glaubrecht. 2004. Multiple origin of viviparity in Southeast Asian gastropods (Cerithioidea: Pachychilidae) and its evolutionary implications. *Evolution* **58**: 2215-2226.
- Köhler, F., S. Panha, and M. Glaubrecht. 2010. Speciation and radiation in a river: Assessing the morphological and genetic differentiation in a species flock of viviparous gastropods (Cerithioidea: Pachychilidae). In: M. Glaubrecht, ed., *Evolution in Action. Case Studies in Adaptive Radiation, Speciation and the Origin of Biodiversity*. Springer, Heidelberg. Pp. 513-550.
- Kondrashov, A. S. and F. A. Kondrashov. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* **311**: 351-353.
- Kondrashov, A. S. and M. V. Mina. 1986. Sympatric speciation: When is it possible? *Biological Journal of the Linnean Society* **27**: 201-223.
- Kondrashov, A. S. and M. Shpak. 1998. On the origin of species by means of assortative mating. *Proceedings of the Royal Society London* **265**: 2273-2278.
- Lack, D. 1947. *Darwin's Finches*. Cambridge University Press, Cambridge, UK.
- Lamarck, J. B. 1809. *Philosophie Zoologique, ou Exposition des Considérations Relatives à l'Histoire Naturelle des Animaux*. 2 vols. Dentu, Paris [In French].
- Lazarus, D. 1983. Speciation in pelagic Protista and its study in the planktonic microfossil record: A review. *Paleobiology* **9**: 327-340.

- Lazarus, D., H. Hilbrecht, C. Spencer-Cervato, and H. Thierstein. 1995. Sympatric speciation and phyletic change in *Globorotalia truncatulinoides*. *Paleobiology* **21**: 28-51.
- Lee, M. S. Y. 2004. The molecularisation of taxonomy. *Invertebrate Systematics* **18**: 1-6.
- Lee, T., H. C. Hong, J. J. Kim, and D. Ó Foighil. 2007. Phylogenetic and taxonomic incongruence involving nuclear and mitochondrial markers in Korean populations of the freshwater snail genus *Semisulcospira* (Cerithioidea: Pleuroceridae). *Molecular Phylogenetics and Evolution* **43**: 386-397.
- Liem, K. F. 1990. Key evolutionary innovations, differential diversity, and symecomorphosis. In: M. H. Nitecki, ed., *Evolutionary Innovations*. University of Chicago Press, Chicago. Pp. 147-170.
- Lind, C. E., B. S. Evans, J. J. U. Taylor, and D. R. Jerry. 2007. Population genetics of a marine bivalve, *Pinctada maxima*, throughout the Indo-Australian Archipelago shows differentiation and decreased diversity at range limits. *Molecular Ecology* **16**: 5193-5203.
- Losos, J. B. 2009. *Lizards in an Evolutionary Tree. Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley.
- Losos, J. B. and R. E. Glor. 2003. Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology and Evolution* **18**: 220-227.
- Losos, J. B. and D. L. Mahler. 2010. Adaptive radiation: The interaction of ecological opportunity, adaptation, and speciation. In: M. Bell, D. Futuyma, W. Eanes, and J. Levinton, eds., *Evolution Since Darwin: The First 150 Years*. Sinauer, Sunderland, Massachusetts. Pp. 381-420.
- Lu, G. and L. Bernatchez. 1999. Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): Support for the ecological speciation hypothesis. *Evolution* **53**: 1491-1505.
- Maddison, E. P. 1997. Gene trees in species trees. *Systematic Biology* **46**: 523-536.
- Malaquias, M. A. E. and D. G. Reid. 2009. Tethyan vivariance, relictualism and speciation: Evidence from a global molecular phylogeny of the opisthobranch genus *Bulla*. *Journal of Biogeography* **36**: 1760-1777.
- Malause, T., M.-T. Bethenod, A. Bontemps, D. Bourguet, J.-M. Cornuet, and S. Ponsard. 2005. Assortative mating in sympatric host races of the European corn borer. *Science* **308**: 258-260.
- Mallet, J. 2001. The speciation revolution. *Journal of Evolutionary Biology* **14**: 887-888.
- Mallet, J. 2004. Poulton, Wallace and Jordan: How discoveries in *Papilio* butterflies led to a new species concept 100 years ago. *Systematics and Biodiversity* **1**: 441-452.
- Mallet, J. 2005. Hybridization as an invasion of the genome. *Trends in Ecology and Evolution* **20**: 229-237.
- Mallet, J. 2008a. Mayr's view of Darwin: Was Darwin wrong about speciation? *Biological Journal of the Linnean Society* **95**: 3-16.
- Mallet, J. 2008b. Hybridization, ecological races and the nature of species: Empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society London (B)* **363**: 2971-2986.
- Martens, K., B. Goddeeris, and G. Coulter, eds., 1994. *Speciation in Ancient Lakes*. Ergebnisse der Limnologie 44. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Maynard Smith, J. 1966. Sympatric speciation. *American Naturalist* **104**: 487-490.
- Mayr, E. 1940. Speciation phenomena in birds. *American Naturalist* **74**: 249-278.
- Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York.
- Mayr, E. 1947. Ecological factors in speciation. *Evolution* **1**: 263-288.
- Mayr, E. 1959. Isolation as an evolutionary factor. *Proceedings of the American Philosophical Society* **103**: 221-230.
- Mayr, E. 1963. *Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Mayr, E. 1982. *The Growth of Biological Thought*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Mayr, E. 1997. *This is Biology*. Harvard University Press, Cambridge, Massachusetts.
- Mayr, E. 1999. An evolutionist's perspective. *The Quarterly Review of Biology* **74**: 401-403.
- Mayr, E. 2001. *What Evolution Is*. Basic Books, New York.
- McCune, A. R. and N. R. Lovejoy. 1998. The relative rate of sympatric and allopatric speciation in fishes. In: D. J. Howard and S. H. Berlocher, eds., *Endless Forms: Species and Speciation*. Oxford University Press, Oxford. Pp. 172-185.
- McKinnon, J. S. and H. D. Rundle. 2002. Speciation in nature: The threespine stickleback model systems. *Trends in Ecology and Evolution* **17**: 480-488.
- McKinnon, J. S., S. Mori, B. K. Blackman, L. David, D. M. Kingsley, L. Jamieson, J. Chou, and D. Schluter. 2004. Evidence for ecology's role in speciation. *Nature* **429**: 294-298.
- McPeck, M. A. and G. A. Wellborn. 1998. Genetic variation and reproductive isolation among phenotypically divergent amphipod populations. *Limnology and Oceanography* **43**: 1169.
- Meier, R. 2008. DNA sequences in taxonomy. Opportunities and challenges. In: Q. D. Wheeler, ed., *The New Taxonomy*. The Systematic Association, special volume series 76. CRC Press, Boca Raton, Florida. Pp. 95-128.
- Mendelson, T. C. and K. L. Shaw. 2005. Rapid speciation in an arthropod. *Nature* **433**: 375.
- Michel, E. 1994. Why snails radiate: A review of gastropod evolution in long-lived lakes, both recent and fossil. In: K. Martens, B. Goddeeris, and G. Coulter, eds., *Speciation in Ancient Lakes*. Ergebnisse der Limnologie 44. Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart. Pp. 285-317.
- Michel, E. 2004. *Vinundu*, a new genus of gastropod (Cerithioidea: 'Thiaridae') with two species from Lake Tanganyika, East Africa, and its molecular phylogenetic relationships. *Journal of Molluscan Studies* **70**: 1-19.
- Michel, E., A. S. Cohen, K. West, M. R. Johnston, and P. W. Kat. 1992. Large African lakes as natural laboratories for evolution: Examples from the endemic gastropod fauna of Lake Tanganyika. *Mitteilungen der Internationalen Vereinigung für Limnologie* **23**: 85-99.
- Michel, E., J. A. Todd, F. R. Cleary, I. Kingma, A. S. Cohen, and M. Genner. 2004. Scales of endemism: Challenges for conservation

- and incentives for evolutionary studies in a gastropod species flock from Lake Tanganyika. *Journal of Conchology, Special Publication* 3: 155-172.
- Mundy, N. I., N. S. Badcock, T. Hart, K. Scribner, K. Janssen, and N. J. Nadeau. 2004. Conserved genetic basis of a quantitative plumage trait involved in mate choice. *Science* 303: 1870-1873.
- Noor, M. A. F. 2002. Is the biological species concept showing its age? *Trends in Ecology and Evolution* 17: 153-154.
- Noor, M. A. F. and J. L. Feder. 2006. Speciation genetics: Evolving approaches. *Nature Reviews Genetics* 7: 851-861.
- Nosil, P. 2008. Ernst Mayr and the integration of geographical and ecological factors in speciation. *Biological Journal of the Linnean Society* 95: 26-46.
- Nosil, P., L. J. Harmon, and O. Seehausen. 2009. Ecological explanations for (incomplete) speciation. *Trends in Ecology and Evolution* 24: 145-156.
- Nyhart, L. 2002. Learning from history: Morphology's challenges in Germany ca. 1900. *Journal of Morphology* 252: 2-14.
- Orr, M. R. and T. B. Smith. 1998. Ecology and speciation. *Trends in Ecology and Evolution* 13: 502-506.
- Ozawa, T., F. Köhler, D. G. Reid, and M. Glaubrecht. 2009. Tethyan relicts on continental coastlines of the northwestern Pacific Ocean and Australasia: Molecular phylogeny and fossil record of batillariid gastropods (Caenogastropoda, Cerithioidea). *Zoologica Scripta* 38: 503-525.
- Palumbi, S. R. 1992. Marine speciation on a small planet. *Trends in Ecology and Evolution* 7: 114-118.
- Palumbi, S. R. 1994. Genetic divergence, reproductive isolation, and marine speciation. *Annual Review in Ecology and Systematics* 25: 547-572.
- Palumbi, S. R. 1996. What can molecular genetics contribute to marine biogeography? An urchin's tale. *Journal of Experimental Marine Biology and Ecology* 203: 75-92.
- Patten, M. A. 2008. The intersection of specialization and speciation. *Journal of Biogeography* 35: 193-194.
- Peterson, A. T., J. Soberon, and V. Sanchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285: 1265-1267.
- Pfenninger, M., S. Staubach, C. Albrecht, B. Streit, and K. Schwenk. 2003. Ecological and morphological differentiation among cryptic evolutionary lineages in freshwater limpets of the nominal form-group *Ancylus fluviatilis* (O. F. Müller, 1774). *Molecular Ecology* 12: 2731-2745.
- Pigeon, D., A. Chouinard, and L. Bernatchez. 1997. Multiple modes of speciation involved in the parallel evolution sympatric morphotypes of Lake Whitefish (*Coregonus clupeaformis*, Salmonidae). *Evolution* 421: 196-205.
- Ponder, W. F. and D. J. Colgan. 2002. What makes a narrow-range taxon? Insights from Australian freshwater snails. *Invertebrate Systematics* 16: 571-582.
- Presgraves, D. C. and S. V. Yi. 2009. Doubts about complex speciation between humans and chimpanzees. *Trends in Ecology and Evolution* 24: 533-540.
- Quesada, H., D. Posada, A. Caballero, P. Morán, and E. Rolán-Alvarez. 2007. Phylogenetic evidence for multiple sympatric ecological diversification in a marine snail. *Evolution* 61: 1600-1612.
- Reid, D. G., K. Lal, J. Mackenzie-Dodds, F. Kaligis, D. T. J. Littlewood, and S. T. Williams. 2006. Comparative phylogeography and species boundaries in *Echinolittorina* snails in the central Indo-West Pacific. *Journal of Biogeography* 33: 990-1006.
- Reid, D. G., P. Dyal, P. Lozouet, M. Glaubrecht, and S. T. Williams. 2008. Mudwhelks and mangroves: The evolutionary history of an ecological association (Gastropoda: Potamididae). *Molecular Phylogenetics and Evolution* 47: 680-699.
- Reid, D. G., P. Dyal, and S. T. Williams. 2010. Global diversification of mangrove fauna: A molecular phylogeny of *Littoraria* (Gastropoda: Littorinidae). *Molecular Phylogenetics and Evolution* 55: 185-201.
- Rensch, B. 1939. Typen der Artbildung. *Biological Review* 14: 180-222 [In German].
- Richards, R. A. 2010. *The Species Problem: A Philosophical Analysis*. Cambridge University Press, Cambridge, UK.
- Rintelen, T. v. and M. Glaubrecht. 2002. Gene trees and species trees – a case study from a species flock of viviparous freshwater gastropods (Caenogastropoda: Cerithioidea: Pachychilidae) from the ancient lakes of Sulawesi, Indonesia. *Abstracts 68th American Malacological Society meeting, Charleston, August 2002*. American Malacological Society, Charleston, South Carolina. P. 110.
- Rintelen, T. v. and M. Glaubrecht. 2005. The anatomy of an adaptive radiation: A unique reproductive strategy in the endemic freshwater gastropod *Tylomelania* (Cerithioidea: Pachychilidae) on Sulawesi, Indonesia, and its biogeographic implications. *Biological Journal of the Linnean Society* 85: 513-542.
- Rintelen, T. v. and M. Glaubrecht. 2006. Rapid evolution of sessility in an endemic species flock of the freshwater bivalve *Corbicula* from ancient lakes on Sulawesi, Indonesia. *Biology Letters* 2: 73-77.
- Rintelen, T. v., A. B. Wilson, A. Meyer, and M. Glaubrecht. 2004. Escalation and trophic specialization drive adaptive radiation of freshwater gastropods in ancient lakes on Sulawesi, Indonesia. *Proceedings of the Royal Society London (Biological Sciences)* 271: 2541-2549.
- Rintelen, T. v., P. Bouchet, and M. Glaubrecht. 2007. Ancient lakes as hotspots of diversity: A morphological review of an endemic species flock of *Tylomelania* (Gastropoda: Cerithioidea: Pachychilidae) in the Malili lake system on Sulawesi, Indonesia. *Hydrobiologia* 592: 11-94.
- Rintelen, T. v., K. v. Rintelen, and M. Glaubrecht. 2010. The species flocks of the viviparous freshwater gastropod *Tylomelania* (Mollusca: Cerithioidea: Pachychilidae) in the ancient lakes of Sulawesi, Indonesia: The role of geography, trophic morphology and color as driving forces in adaptive radiation. In: M. Glaubrecht, ed., *Evolution in Action. Case Studies in Adaptive Radiation, Speciation and the Origin of Biodiversity*. Springer, Heidelberg. Pp. 485-512.
- Rossiter, A. and H. Kawanabe. 2000. *Ancient Lakes: Biodiversity, Ecology and Evolution*. Academic Press, San Diego.
- Rundle, H. D. and P. Nosil. 2005. Ecological speciation. *Ecology Letters* 8: 336-352.
- Rundle, H. D. and M. C. Whitlock. 2001. A genetic interpretation of ecologically dependent isolation. *Evolution* 55: 198-201.

- Rundle, H. D., L. Nagel, J. W. Boughman, and D. Schluter. 2000. Natural selection and parallel speciation in sympatric sticklebacks. *Science* **287**: 306-308.
- Salzburger, W. and A. Meyer. 2004. The species flocks of East African cichlid fishes: Recent advances in molecular phylogenetics and population genetics. *Naturwissenschaften* **91**: 277-290.
- Salomon, M. 2001. Evolutionary biogeography and speciation: Essay on a synthesis. *Journal of Biogeography* **28**: 13-27.
- Schilthuizen, M. 2001. *Frogs, Flies and Dandelions. The Making of Species*. Oxford University Press, Oxford.
- Schneider, C. J., T. B. Smith, B. Larison, and C. Moritz, 1999. A test of alternative models of diversification in tropical rainforests: Ecological gradients versus rainforest refugia. *Proceedings of the National Academy of Sciences* **96**: 13869-13873.
- Schliwen, U. K. and B. Klee. 2004. Reticulate sympatric speciation in Cameroonian crater lake cichlids. *Frontiers in Zoology* **1**: 5.
- Schliwen, U. K., D. Tautz, and S. Pääbo. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* **368**: 629-632.
- Schliwen, U. K., K. Rassmann, M. Markmann, J. A. Markert, T. D. Kocher, and D. Tautz. 2001. Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham, Cameroon. *Molecular Ecology* **10**: 1471-1488.
- Schliwen, U. K., T. D. Kocher, K. R. McKaye, O. Seehausen, and D. Tautz. 2006. Evidence for sympatric speciation? *Nature* **447**: E12-E13.
- Schluter, D. 1996. Ecological causes of adaptive radiation. *The American Naturalist* **148**: 40-63.
- Schluter, D. 2000a. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- Schluter, D. 2000b. Ecological character displacement in adaptive radiation. *The American Naturalist* **156**: 4-16.
- Schluter, D. 2001. Ecology and the origin of species. *Trends in Ecology and Evolution* **16**: 372-380.
- Schluter, D. 2009. Evidence for ecological speciation and its alternative. *Science* **323**: 737-741.
- Schluter, D. and L. M. Nagel. 1995. Parallel speciation by natural selection. *American Naturalist* **146**: 292-301.
- Schluter, D., J. W. Boughman, and J. W. Rundle. 2001. Parallel speciation with allopatry. *Trends in Ecology and Evolution* **16**: 283-284.
- Scholz, H. and M. Glaubrecht. 2007. *Melanoides* from Lake Turkana: A documentation of speciation and case study for "punctuated equilibrium"? *Abstracts World Congress of Malacology, Antwerp July 2007* Antwerp, Unitas Malacologia. Pp. 197-198.
- Scholz, H., J. C. A. Joordens, and M. Glaubrecht. 2009. Turkana Basin molluscs revisited: The theory of punctuated equilibrium on trial. *Abstracts Systematics, 1st meeting of Biosyst EU*, Leiden, The Netherlands. P. 116.
- Schwenk, K., N. Brede, and B. Streit. 2008. Introduction. Extent, process and evolutionary impact of interspecific hybridization in animals. *Philosophical Transactions of the Royal Society London (B)* **363**: 2805-2810.
- Seehausen, O. 2004. Hybridization and adaptive radiation. *Trends in Ecology and Evolution* **19**: 198-207.
- Seehausen, O. 2006. African cichlid fish: A model system in adaptive radiation research. *Proceedings of the Royal Society* **273**: 1987-1998.
- Seehausen, O., Y. Terai, I. S. Magalhaes, K. L. Carleton, H. D. J. Mrosso, R. Miyagi, I. van der Sluijs, M. Schneider, M. E. Maan, H. Tachida, H. Imai, and N. Okada. 2008. Speciation through sensory drive in cichlid fish. *Nature* **455**: 620-626.
- Sengupta, M. E., T. K. Kristensen, H. Madson, and A. Joergensen. 2009. Molecular phylogenetic investigations of the Viviparidae (Gastropoda: Caenogastropoda) in the lakes of the Rift Valley area of Africa. *Molecular Phylogenetics and Evolution* **52**: 797-805.
- Sepkoski, D. and M. Ruse, eds. 2009. *The Paleobiological Revolution. Essays on the Growth of Modern Paleontology*. University of Chicago Press, Chicago.
- Shaw, K. L. 2002. Conflict between nuclear and mitochondrial DNA phylogenies of a recent species radiation: What mtDNA reveals and conceals about modes of speciation in Hawaiian crickets. *Proceedings of the National Academy of America* **99**: 16122-16127.
- Shaw, K. L. and P. D. Danley. 2003. Behavioral genomics and the study of speciation at a porous species boundary. *Zoology* **106**: 261-273.
- Shaw, P. W., G. F. Turner, M. Rizman Idid, R. L. Robinson, and G. R. Carvalho. 2000. Genetic population structure indicates sympatric speciation of Lake Malawi pelagic cichlids. *Proceedings of the Royal Society of London (B)* **267**: 2273-2280.
- Simpson, G. G. 1953. *The Major Features of Evolution*. Columbia University Press, New York.
- Sites, J. W. and J. C. Marshall. 2003. Delimiting species: A renaissance issue in systematic biology. *Trends in Ecology and Evolution* **18**: 462-470.
- Sites, J. W. and J. C. Marshall. 2004. Operational criteria for delimiting species. *Annual Review of Ecology, Evolution and Systematics* **35**: 199-227.
- Smith, T. B., R. K. Wayne, D. Girman, and M. W. Bruford. 1997. A role for ecotones in generating rainforest biodiversity. *Science* **276**: 1855-1857.
- Sorenson, M. D., K. M. Sefc, and R. B. Payne. 2003. Speciation by host switch in brood parasitic indigobirds. *Nature* **424**: 928-931.
- Strong, D. R. and F. Köhler. 2009. Morphological and molecular analysis of '*Melania*' *jacqueti* Dautzenberg and Fischer, 1906: From anonymous orphan to critical basal offshoot of the Semisulcospiridae (Gastropoda: Cerithioidea). *Zoologica Scripta* **38**: 483-502.
- Strong, E. E., D. J. Colgan, J. M. Healy, C. Lydeard, W. F. Ponder, and M. Glaubrecht. 2011. Phylogeny of the gastropod superfamily Cerithioidea using morphology and molecules. *Zoological Journal Linnean Society London*, doi: 10.1111/j.1096-3642.2010.00670.x.
- Sudhaus, W. 2004. Radiation within the framework of evolutionary ecology. *Organisms, Diversity and Evolution* **4**: 127-134.
- Tatarenkov, A. and K. Johannesson. 1998. Evidence of a reproductive barrier between two forms of the marine periwinkle *Littorina fabalis* (Gastropoda). *Biological Journal of the Linnean Society* **63**: 349-365.

- Turner, T. L. and M. W. Hahn. 2010. Genomic islands of speciation or genomic islands *and* speciation? *Molecular Ecology* **19**: 848-850.
- Venditti, C. and M. Pagel. 2009. Speciation as an active force in promoting genetic evolution. *Trends in Ecology and Evolution* **25**: 14-20.
- Venditti, C., A. Meade, and M. Pagel. 2010. Phylogenies reveal new interpretation of speciation and the Red Queen. *Nature* **463**: 349-352.
- Via, S. 2001. Sympatric speciation in animals: The ugly duckling grows up. *Trends in Ecology and Evolution* **16**: 381-390.
- Via, S. and D. J. Hawthorne. 2002. The genetic architecture of ecological specialization: Correlated gene effects on host use and habitat choice in pea aphids. *American Naturalist* **159**: 76-88.
- Waga, W., D. Mackiewicz, M. Zawierta, and S. Cebrat. 2007. Sympatric speciation as intrinsic property of the expanding population. *Theory Bioscience* **126**: 53-59.
- Wake, D. B. 1997. Incipient species formation in salamanders of the *Ensatina* complex. *Proceedings of the National Academy of Sciences* **94**: 7761-7767.
- Walther, A., T. Lee, J. B. Burch, and D. Ó. Foighil, 2006. *E pluribus unum*: A phylogenetic and phylogeographic reassessment of *Laevapex* (Pulmonata: Ancyliidae), a North American genus of freshwater limpets. *Molecular Phylogenetics and Evolution* **40**: 501-516.
- Wares, J. P. and T. F. Turner. 2003. Phylogeography and diversification in aquatic mollusks. In: C. Lydeard and D. R. Lindberg, eds., *Molecular Systematics and Phylogeography of Mollusks*. Smithsonian Books, Washington, D.C. Pp. 229-269.
- Wesenberg-Lund, C. 1939. *Biologie der Süßwassertiere. Wirbellose Tiere*. Julius Springer, Wien [In German].
- West, K., A. S. Cohen, and M. Baron. 1991. Morphology and behaviour of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator-prey coevolution. *Evolution* **45**: 589-607.
- West, K. and A. S. Cohen, 1994. Predator-prey coevolution as a model for the unusual morphologies of the crabs and gastropods of Lake Tanganyika. In: K. Martens, B. Goddeeris, and G. Coulter, eds., *Speciation in Ancient Lakes*. Ergebnisse der Limnologie 44. Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart. Pp. 267-283.
- West, K. and A. S. Cohen. 1996. Shell microstructure of gastropods from Lake Tanganyika, Africa: Adaptation, convergent evolution, and escalation. *Evolution* **50**: 672-681.
- West, K. and E. Michel. 2000. The dynamics of endemic diversification: Molecular phylogeny suggests an explosive origin of the thiarid gastropods of Lake Tanganyika. In: A. Rossiter and H. Kawanabe, eds., *Ancient Lakes: Biodiversity, Ecology and Evolution*. Advances in Ecological Research 31. Academic Press, San Diego. Pp. 331-354.
- Whelan, S., P. Liò, and N. Goldman. 2001. Molecular phylogenetics: State-of-the-art methods for looking into the past. *Trends in Ecology and Evolution* **17**: 262-272.
- Wilding, C. S., R. K. Butlin, and J. Grahame. 2001. Differential gene-exchange between morphs of *Littorina saxatilis* detected using AFLP markers. *Journal of Evolutionary Biology* **14**: 611-619.
- Wilke, T., R. Väinölä, and F. Riedel, eds. 2008. *Patterns and Processes of Speciation in Ancient Lakes: Proceedings of the Fourth Symposium on Speciation in Ancient Lakes, Berlin, Germany*. Developments in Hydrobiology. Springer, Heidelberg, Berlin.
- Wilke, T., M. Benke, M. Brändle, C. Albrecht, and J.-M. Bichain. 2010. The neglected side of the coin: Non-adaptive radiations in spring snails (*Bythinella* spp.). In: M. Glaubrecht, ed., *Evolution in Action. Case Studies in Adaptive Radiation and the Origin of Biodiversity*. Special volume from the SPP 1127 "Radiations – Genesis of Biological diversity" of the DFG. Springer, Heidelberg, Berlin. Pp. 551-578.
- Williams, S. T. and T. F. Duda. 2008. Did tectonic activity stimulate Oligo-Miocene speciation in the Indo-West Pacific? *Evolution* **62**: 1618-1634.
- Williams, S. T. and D. G. Reid. 2004. Speciation and diversity on tropical rocky shores: A global phylogeny of snails of the genus *Echinolittorina*. *Evolution* **58**: 2227-2251.
- Williams, S. T., D. G. Reid, and D. T. J. Littlewood. 2003. A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): Unequal evolutionary rates, morphological parallelism and biogeography of the Southern Ocean. *Molecular Phylogenetics and Evolution* **28**: 60-86.
- Williamson, P. G. 1981. Palaeontological documentation of speciation in Cenozoic molluscs from Turkana Basin. *Nature* **293**: 437-443.
- Williamson, P. G. 1985. Punctuated equilibrium, morphological stasis and the palaeontological documentation of speciation: A reply to Fryer, Greenwood and Peake's critique of the Turkana Basin mollusc sequence. *Biological Journal of the Linnean Society* **26**: 307-324.
- Wilkins, J. S. 2009. *Species. A History of the Idea*. University of California Press, Berkeley.
- Wilson, A. B., K. Noack-Kunmann, and A. Meyer. 2000. Incipient speciation in sympatric Nicaraguan crater lake cichlid fishes: Sexual selection versus ecological diversification. *Proceedings of the Royal Society of London (B)* **267**: 2133-2141.
- Wilson, A. B., M. Glaubrecht, and A. Meyer. 2004. Ancient lakes as evolutionary reservoirs: Evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society of London (B)* **271**: 529-536.
- Wu, C.-I. 2001. The genic view of the process of speciation. *Journal of Evolutionary Biology* **14**: 851-865.
- Zachos, F. 2009. Gene trees and species trees – mutual influence and interdependences of population genetics and systematics. *Journal of Zoological Systematics and Evolutionary Research* **47**: 209-218.
- Zimmermann, E. C. 1958. Three hundred species of *Drosophila* in Hawaii? A challenge to geneticists and evolutionists. *Evolution* **12**: 557-558.

Submitted: 15 September 2010; **accepted:** 29 November 2010;
final revisions received: 9 February 2011